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Cooperative Investigations of the Caribbean and Adjacent Regions – II

SYMPOSIUM ON PROGRESS IN MARINE RESEARCH IN THE CARIBBEAN AND ADJACENT REGIONS

Held in Caracas, 12-16 July 1976

Papers on fisheries, aquaculture and marine biology

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Investigaciones Cooperativas del Caribe y Regiones Adyacentes – II

SIMPOSIO SOBRE ADELANTOS EN LAS INVESTIGACIONES MARINAS EN EL CARIBE Y REGIONES ADYACENTES

celebrado en Caracas, 12-16 de julio de 1976

Contribuciones sobre pesquerías, acuicultura y biología marina

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ORGANIZACION DE LAS NACIONES UNIDAS PARA LA AGRICULTURA Y LA ALIMENTACION

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Edited by
Redactado por
Harris B. Stewart, Jr.

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ORGANIZACION DE LAS NACIONES UNIDAS PARA LA AGRICULTURA Y LA ALIMENTACION

Rome, December 1977
Roma, Diciembre 1977

PREPARATION OF THIS REPORT

This publication forms part of the Proceedings of the Symposium on Advances in Marine Research in the Caribbean and Adjacent Regions (CICAR-II Symposium) held in Caracas, Venezuela, 6-12 July 1976. The Symposium was the conclusion of the international programme Cooperative Investigations of the Caribbean and Adjacent Regions. The present volume, issued by FAO in its Fisheries Reports series, contains the full texts in their original language of papers on fisheries, marine biology and aquaculture. Papers on physical and chemical oceanography, marine geology and geophysics will be published by IOC (Unesco).

PREPARACIÓN DE ESTE DOCUMENTO

Esta publicación forma parte de las Actas del Simposio sobre Adelantos en Investigaciones Marinas en el Mar Caribe y Regiones Adyacentes (Simposio CICAR-II), que tuvo lugar en Caracas, Venezuela, del 12 al 16 de julio de 1976. El Simposio fue la conclusión del programa internacional Investigaciones Cooperativas del Mar Caribe y Regiones Adyacentes. El presente volumen, editado por la FAO en su serie de Informes de Pesca, contiene el texto íntegro en su lengua original de las comunicaciones sobre pesquerías, biología marina y acuicultura. Las comunicaciones sobre oceanografía física y química, geología marina y geofísica, y meteorología, serán publicadas por la COI (Unesco).

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FOREWORD

The CICAR-II Symposium, held in Caracas, Venezuela in July 1976, was called to present the advances in marine research achieved during the period of the Cooperative Investigations of the Caribbean and Adjacent Regions (CICAR), 1968-1975. The Symposium was sponsored by the Intergovernmental Oceanographic Commission (IOC), a part of the United Nations Educational, Scientific and Cultural Organization, (Unesco) with the assistance of the Food and Agriculture Organization (FAO) and the World Meteorological Organization (WMO). The Government of Venezuela generously provided facilities and made local arrangements for the proceedings.

The success of the Symposium was the result of the efforts of many people in countries throughout the region, of whom only a few can be mentioned here. The programme was organized by an International Steering Committee of which H.B. Steward, Jr. (U.S.A.) was Chairman and the members were A. Ayala Castañares (Mexico), I. Emilsson (Unesco/Mexico), I. Goodbody (Jamaica), A. Mena M. (Cuba), R. Molinari (U.S.A.), H. Pérez Nieto (Venezuela), H. Postma (SCOR/Netherlands), T. Rass (USSR) and T. van't Hof (Netherlands). The Local Arrangements Committee in Venezuela was headed by J.A. Galavís S., and included H. Pérez Nieto, J. d'Angelo B. and A. Ahmad. The International Coordinator of CICAR, J.S. Kenny (Trinidad and Tobago), served as Chairman of the Symposium.

This volume, published by FAO, contains the papers on fisheries, aquaculture and marine biology presented at the Symposium. Papers on physical oceanography, marine geology and geophysics, chemical oceanography, meteorology and air-sea interactions appear in a separate volume published by Unesco.

The papers in English in this volume were edited by John H. Wickstead (United Kingdom), those in Spanish by Pablo Penchaszadeh and Juan José Salaya (Venezuela).

Enquiries concerning the content of the papers should be directed to the authors.

Harris B. Stewart, Jr.
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PREAMBULO

El Simposio CICAR-II, celebrado en Caracas, Venezuela, en julio de 1976, se convocó para presentar los adelantos consequidos en materia de investigaciones marinas durante el período de las Investigaciones cooperativas en el mar Caribe y regiones adyacentes (ICCRA), 1968-1975. El simposio fue patrocinado por la Comisión Oceanográfica Intergubernamental (COI), y una parte de la Organización de las Naciones Unidas para la Educación, la Ciencia y la Cultura (Unesco), y tuvo colaboración de la Organización de las Naciones Unidas para la Agricultura y la Alimentación (FAO) y la Organización Meteorológica Mundial (OMM). El Gobierno de Venezuela proporcionó generosamente las instalaciones y servicios, y se hizo cargo de los preparativos locales.

El buen éxito del simposio se debió a los esfuerzos de muchas personas de diversos paises de la región, de las cuales tan sólo algunas pueden mencionarse en el presente documento. El programa fue organizado por el Comité Organizador Internacional, cuyo Director era H.B. Stewart, Jr. (EE.UU.), y cuyos miembros eran A. Ayala Castañares (México), I. Emilsson (Unesco/México), I. Goodbody (Jamaica), A. Mena M. (Cuba), R. Molinari (EE.UU.), H. Pérez Nieto (Venezuela), H. Postma (CCIO/Países Bajos), T. Rass (U.R.S.S.) y T. van't Hof (Países Bajos). El Comité Organizador Venezolano estuvo presidido por J.A. Galavís S., y de él formaban parte H. Pérez Nieto, J. d'Angelo B. y A. Ahmad. El Coordinador Internacional del ICCRA, J.S. Kenny (Trinidad y Tabago), actuó como Presidente del simposio.

Este volumen, publicado por la FAO, contiene los documentos relativos a pesca, acuicultura y biología marina presentados en el simposio. Los documentos que tratan sobre oceanografía física, geología marina y geofísica, oceanografía química, meteorología e interacción aire-mar figuran en un volumen separado publicado por la Unesco.

Los documentos que aparecen en inglés en el presente volumen fueron editados por John H. Wickstead (Reino Unido), y los que aparecen en español por Pablo Penchaszadeh y Juan José Salaya (Venezuela).

Las solicitudes de información sobre el contenido de los documentos deberán dirigirse a los autores de los mismos.

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CRECIMIENTO E INDICE DE ENGORDE DEL MEJILLON Perna perna (L) CULTIVADO EN EL GOLFO DE CARIACO, VENEZUELA

por

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Instituto Oceanográfico, Universidad de Oriente,
Cumaná, Venezuela

CONTENIDO

1. INTRODUCCION
2. SITUACION GEOGRAFICA DEL AREA DE TRABAJO
3. MATERIALES Y METODOS
4. CRECIMIENTO
5. INDICE DE ENGORDE
6. SALINIDAD, TEMPERATURA, OXIGENO Y PRODUCTIVIDAD PRIMARIA
7. DISCUSION Y CONCLUSIONES
8. REFERENCIAS

Resumen

En un intento por mejorar la eficiencia del cultivo del mejillón Perna perna (L) en el Golfo de Cariaco, mediante el sistema de balsas flotantes, se ha estudiado el crecimiento y la variación estacional del "índice de engorde" de la semilla, durante el período comprendido entre julio de 1973 y junio de 1974. El crecimiento se estudió siguiendo los desplazamientos mensuales del valor modal de las distribuciones de frecuencias de tallas (distancia antero-posterior). Como índice de engorde se utilizó la razón del peso de la carne en g deshidratada al volúmen intervalvar en ml. La tasa de crecimiento fue de 51 mm por año, observándose el crecimiento máximo en los meses comprendidos entre febrero y septiembre y el mínimo en los meses de diciembre y enero. En general, los valores más altos del índice de engorde se encontraron en el périodo de crecimiento óptimo. Aparentemente, los períodos de crecimiento y de engorde siguieron las fluctuaciones de los organismos fitoplanctónicos, pero probablemente, también están asociados con el ciclo reproductivo del mejillón.

Abstract

In order to improve the efficiency in culturing the mussel Perna perna (L) in the Gulf of Cariaco, growth and seasonal variations of the "condition index" of the "seed" (newly settled mussels) have been studied on rafts from July 1973 to June 1974. Growth was studied by analysing the monthly progression of modal values in the distribution of size frequencies (antero-posterior or valve length). As the condition index the relation between the weight of the dehydrated meat (in g) to the intervalve volume (in ml) was used. Annual growth rate was 51 mm with the maximum growth rate from February to September and the minimum from December to January. In general, the highest values of condition factor were observed during the optimal growth period. Apparently, growth and fattening periods of the mussel Perna perna followed the fluctuations of phytoplankton and probably also its own reproduction cycle.

1. INTRODUCCION

El mejillón Perna perna (L), pertenece a la familia Mytilidae Rafinesque, 1815. Esta especie fue descrita originalmente para el Estrecho de Magallanes, pero es común a lo largo de la costa Atlántica Sudamericana desde Uruguay hasta el área del Caribe. A pesar de que la pesquería de este molusco es relativamente pequeña (FAO, 1972), en Venezuela ocupa lugar importante en la región oriental en donde se encuentran ubicados los bancos naturales. De estos, los más productivos se encuentran a lo largo de la costa norte del Estado Sucre entre Manzanillo y el Morro de Puerto Santo, y son los que preveen la semilla para las balsas de cultivo ubicadas principalmente en el Golfo de Cariaco, cerca de Cumaná.

El cultivo de mejillones en Venezuela, es parecido al que se lleva a cabo en las Rías Gallegas. Los cultivos experimentales iniciales se llevaron a cabo en el Mar Caribe a lo largo de la costa rocosa cerca de Carúpano. Sin embargo, factores adversos conspiraron contra el establecimiento de esta industria. Las balsas fueron dañadas por marejadas fuertes durante la estación de vientos y algunas cosechas se perdieron debido a mareas rojas.

Las operaciones de cultivo en el Golfo de Cariaco comienzan cuando los mejillones juveniles (semilla), 2,5-3,5 cm de largo, son adheridos a cuerdas de sisal o varas de guatacare (Beureria cumanensis) por medio de vendas de rayón hasta que ellos se adhieren en forma definitiva a las varas o cuerdas que varían en longitud de 4,5-6,5 y cuelgan de balsas flotantes. La cosecha de estos mejillones se efectúa 8-10 meses después. Los rendimientos varían de acuerdo con la longitud de la cuerda de 50 a 80 kg por cuerda. Estos rendimientos son de 3 a 5 veces más altos que los reportados en las operaciones españolas (Ryther y Bardach, 1968).

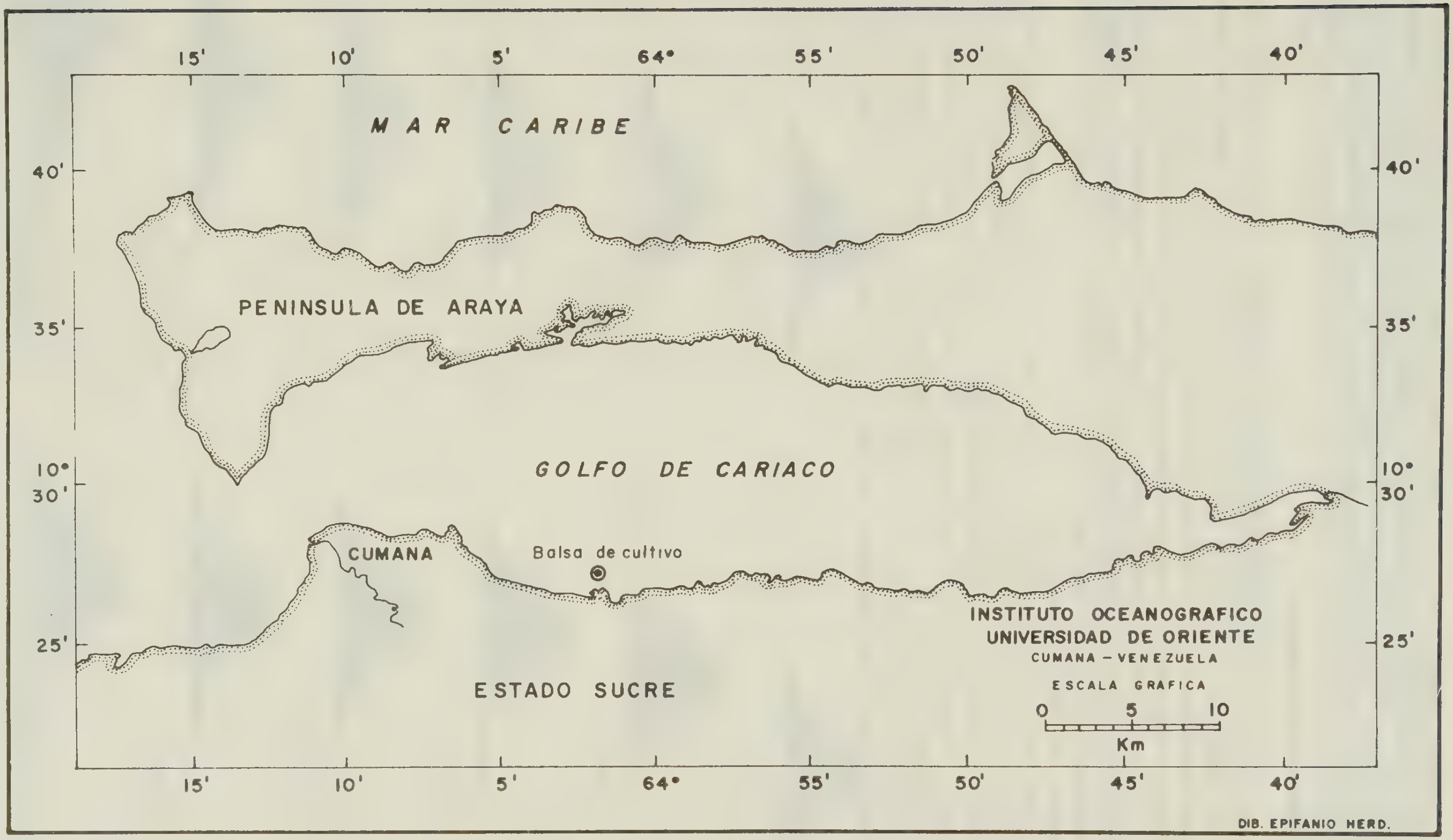
La producción de mejillones cultivados en las costas orientales de Venezuela alcanzó la cifra de 94 t en 1971. Esta producción aumentó hasta 260 t en 1973. Esta producción ha sido absorbida por el mercado interno

La calidad de los productos pesqueros juega un papel muy importante en el proceso económico de la oferta y la demanda. En los bivalvos uno de los métodos más satisfactorios para evaluarla es la determinación del índice de engorde (Hopkins, 1949). El término engorde se refiere a la proporción de partes blandas, en volumen y peso, que ocupa la cavidad intervalvar. Vélez (1971) determinó, durante un ciclo anual, la fluctuación mensual del engorde en Perna perna, aunque el mismo autor sugiere la necesidad de repetir el estudio para determinar el verdadero patrón de fluctuación del engorde de estos mejillones. Carvajal (1969) efectuó observaciones sobre el crecimiento de los mejillones de los bancos naturales, allí hizo observaciones del crecimiento medio mensual, períodos de menor crecimiento y sus probables causas.

Con el presente trabajo se pretenden alcanzar los siguientes objetivos: primero, conocer la tasa mensual de crecimiento y el crecimiento absoluto, y segundo, establecer las variaciones mensuales de su índice de engorde.

2. SITUACION GEOGRAFICA DEL AREA DE TRABAJO

El Golfo de Cariaco está situado en la región nororiental de Venezuela, entre los 10° 26' 19" y los 10° 34' 53" de latitud norte y los 63° 38' 45" y los 64° 13' 00" de longitud oeste. Tiene 56 km de largo y un ancho máximo de 14 km aunque solo tiene 3 km de ancho en su entrada (Fig. 1). Su cuenca tiene una profundidad máxima de 90 m. Está influenciado por vientos alisios fuertes estacionales que soplan principalmente del nor-este y este, entre noviembre y mayo. Los vientos alisios del noroeste, desplazan el agua de la superficie del Golfo y esto trae afloramiento (FAO/UN, 1963).


MAR CARIBE
PENINSULA DE ARAYA
GOLFO DE CARIACO
CUMANA
Balsa de cultivo
ESTADO SUCRE
INSTITUTO OCEANOGRAFICO
UNIVERSIDAD DE ORIENTE
CUMANA - VENEZUELA
ESCALA GRAFICA
0
5
10
Km
15'
10'
5'
64°
55'
50'
45'
40'
40'
35'
10°
30'
25'

DIB. EPIFANIO HERD.

FIG. I AREA GEOGRAFICA DE TRABAJO

3. MATERIALES Y METODOS

Las muestras fueron tomadas de una balsa semicomercial perteneciente al Instituto Oceanográfico de la Universidad de Oriente, fondeada en el área descrita anteriormente. Esta balsa consiste en una estructura flotante sustentada por seis flotadores de madera revestidos de concreto por su parte exterior, con una superficie de trabajo de 336 m^2. Está anclada y sujeta por un grillete giratorio que le permite orientarse en dirección de la corriente o el viento predominante.

Los mejillones juveniles fueron adheridos a cuerdas de sisal, a una densidad de 3 000 por cuerda. El tamaño de la semilla con la que se inició la siembra fue determinado una vez colocadas las cuerdas en las balsas, obteniéndose una talla promedio de 3,39 cm. Las tasas de crecimiento mensual fueron determinadas por muestreos quincenales en nueve cuerdas distribuidas a lo largo y ancho de la balsa. El procedimiento consistió en muestrear 60 mejillones por cuerda a tres profundidades diferentes, obteniéndose 1 080 mejillones cada mes. El crecimiento se analizó mediante el desplazamiento del valor modal de la distribución de frecuencias de talla (Fig. 2).

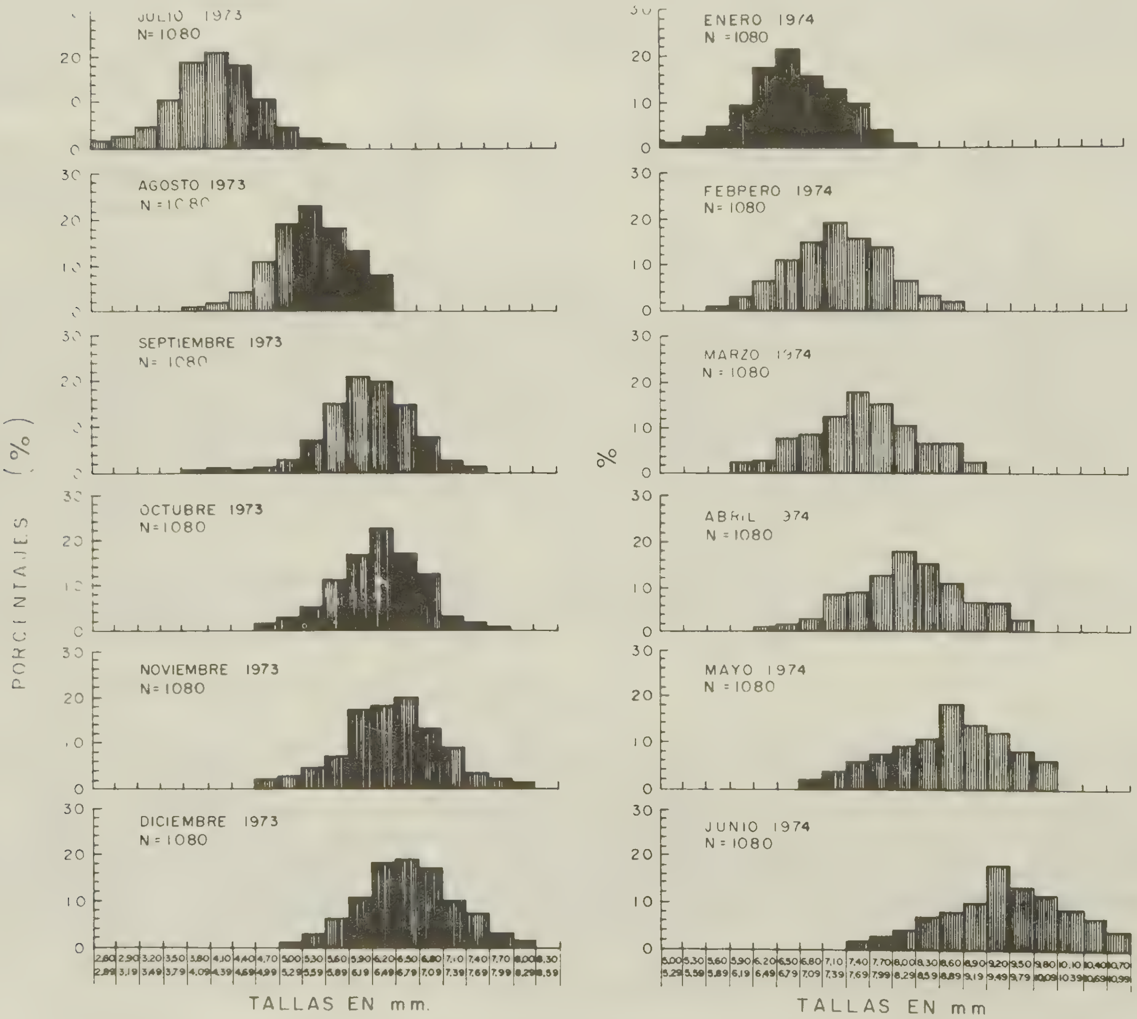


FIG 2 DISTRIBUCION PORCENTUAL MENSUAL DE LAS FRECUENCIAS DE TALLAS DE LOS MEJILLONES

Los muestreos para la determinación del índice de engorde consistieron en 30 mejillones de 7 a 8 cm tomados de las cuerdas de la parte anterior de la balsa. Para estos propósitos se considera la parte anterior como aquella por donde está sujeta la balsa. El índice se determinó de acuerdo al método descrito por Korringa (1955) y evaluado por Baird (1958). El volumen intervalval se obtuvo de la diferencia entre el volumen total y el volumen de las valvas. La carne una vez retirada de las conchas fue deshidratada a 100 °C durante 48 h (Ingle, 1949; Sakuda, 1966), después de lo cual se pesó. El índice de engorde fue luego determinado mediante la fórmula:

$$\text{Indice de engorde} = \frac{\text{Peso de la carne deshidratada (g)}}{\text{Volumen intervalvar (ml)}} \times 100$$

4. CRECIMIENTO

El valor modal inicial fue de 4,25 cm y el final de 9,35 cm lo cual corresponde a una tasa de crecimiento anual de 5,10 cm.

La representación gráfica de los valores modales de la distribución mensual de la frecuencia de tallas (Fig. 3), durante el ciclo anual estudiado (1973-74), presenta dos períodos de crecimiento: el primero de julio a septiembre de 1973 con tasas de crecimiento mensual comprendidas entre 0,60 cm y 1,20 cm; el segundo período de febrero a junio de 1974, con tasas de crecimiento mensual comprendidas entre 0,30 y 0,60 cm. Durante los meses de octubre y noviembre las tasas de crecimiento fueron de 0,30 cm y en diciembre de 1973 y enero de 1974 no se observaron incrementos de talla, permaneciendo los valores modales en la misma posición.

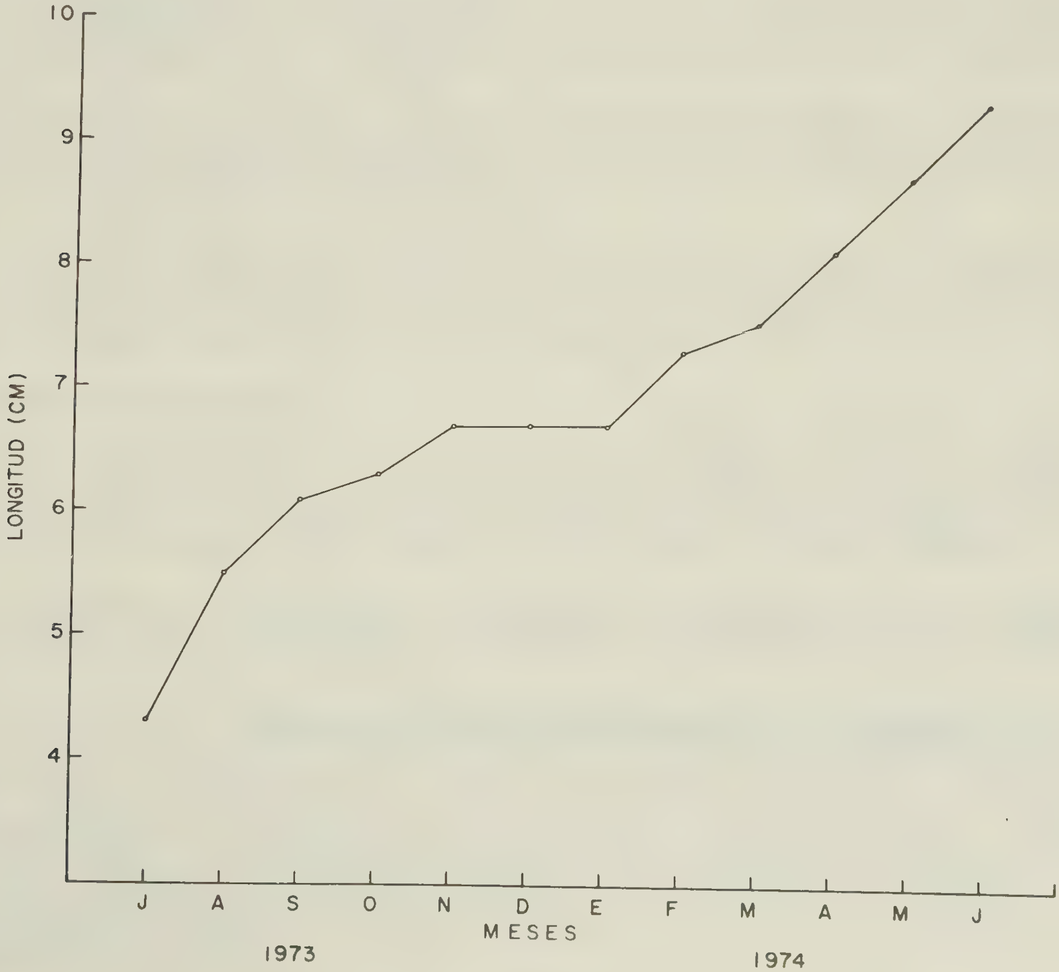


FIG. 3 VALORES MODALES DE LA DISTRIBUCION MENSUAL DE LA FRECUENCIA DE TALLAS

5. INDICE DE ENGORDE

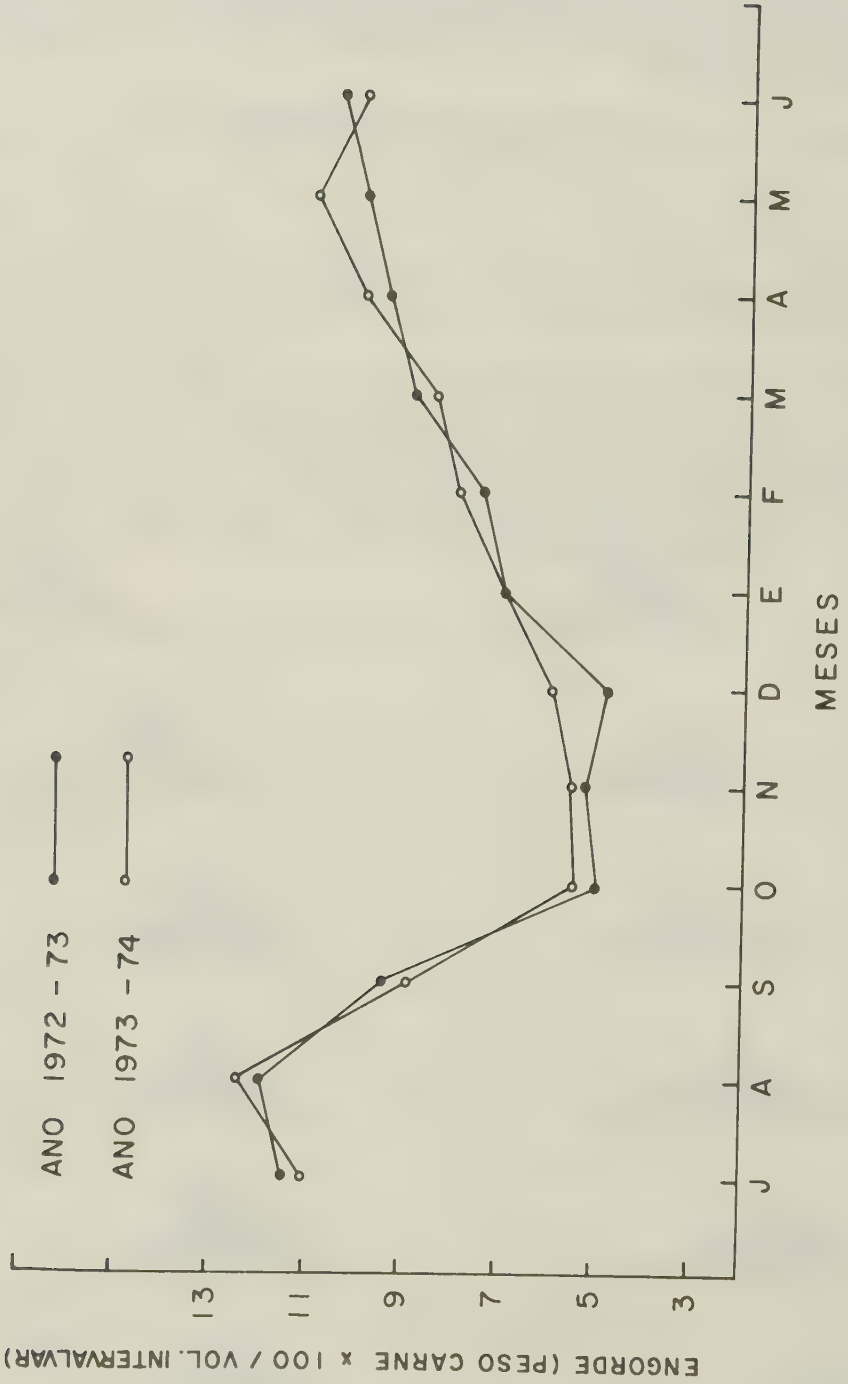


FIG. 4 FLUCTUACION MENSUAL DE ENGORDE

Para el período 1972-73, la curva que presenta los valores del índice de engorde experimenta un ascenso en los meses de julio a agosto seguido de un descenso gradual hasta octubre. En este mismo mes se inicia un período de recuperación que concluye en noviembre desde donde decrece hasta diciembre. De este mes en adelante se reinicia el período de recuperación, ascendiendo gradualmente hasta el mes de junio.

En el período 1973-74 también se observa un ascenso de la curva en los meses de julio a agosto, seguido de un descenso gradual hasta octubre. A partir de esta fecha, el mejillón se recupera ininterrumpidamente hasta el mes de mayo de 1974, donde decrece un poco hasta junio del mismo año. El engorde durante este período evidentemente presentó menos fluctuaciones que el período anterior. En general, las fluctuaciones del índice de engorde presentaron una tendencia general en los dos períodos de tiempo estudiados (1972-73, 1973-74).

Es muy importante señalar que, durante los dos años estudiados, los valores máximos se presentaron en el mes de agosto. Los valores mínimos se ubicaron en el mes de diciembre para el período 1972-73, y el mes de octubre para el período 1973-74.

Si se asume que los mejillones tienen una condición comercial aceptable cuando alcanzan un valor de 9 en la escala de valores encontrados en el "índice", podemos definir claramente dos períodos de engorde en los cuales los mejillones pueden considerarse comercialmente aceptables. El primer período estaría entre julio y septiembre y el segundo entre marzo y junio, en los dos anos estudiados.

6. SALINIDAD, TEMPERATURA, OXIGENO Y PRODUCTIVIDAD PRIMARIA

El Golfo de Cariaco puede ser considerado como un cuerpo de agua isohalino. La salinidad en el sitio de cultivo fluctuó entre 36,47 y 36,78 por ciento durante el período de trabajo. La temperatura del agua para el mismo período varió de 24,2° a 28,2° C en la superficie y de 21,6° a 27,7° C a la profundidad donde terminaban las cuerdas de cultivo (6,5 m).

En la superficie del agua, el oxígeno disuelto siempre se mantuvo por encima del porcentaje de saturación. Sin embargo, cerca de fondo (18 m) el oxígeno disuelto constituye sólo el 50 por ciento de saturación, posiblemente ello se deba a la alta producción y subsecuente descomposición de la materia orgánica.

En términos de productividad primaria, el Golfo de Cariaco puede ser descrito como una zona de surgencia (Ryther, 1969). En el área estudiada la productividad primaria fluctuó de 0,1 a 2,34 gC/m^2/día, representando un rendimiento potencial de 235 gC/m^2/año para una columna de agua de 10 m de profundidad (Mandelli y Acuna, 1973).

7. DISCUSION Y CONCLUSIONES

Los resultados obtenidos en el presente trabajo indican claramente que durante la evolución de la cosecha mejillonera 1973-74, hubo dos períodos bien definidos, comprendidos entre julio y septiembre de 1973 y entre febrero y junio de 1974 donde la tasa de crecimiento fue más alta. Ambos períodos están separados por otro de baja tasa de crecimiento.

Por otra parte, la fluctuación del índice de engorde tiende a presentar características muy semejantes a la del crecimiento. Los períodos de engorde son de julio a septiembre el primero y de marzo a junio el segundo.

Carvajal (1969) estudió el crecimiento de Perna perna en los bancos naturales, señalando el inicio de su experiencia con tallas que promediaban 5,1 mm de largo por 3,3 mm de alto, continuando sus observaciones hasta alcanzar tallas medias de 74,5 mm de largo por 39,2 mm de alto. No señala los períodos de crecimiento óptimo, pero señala que los menores incrementos coincidieron con la presencia de aguas rojas en los meses de agosto y principios de septiembre, cuando se sucedió una mortalidad masiva que impidió la continuación de los estudios. Estos resultados no presentan semejanza con los encontrados por nosotros ya que durante el presente estudio no se observaron mareas rojas que pudiesen interferir en el normal crecimiento de los mejillones.

Vélez (1971) estudiando la variación del índice de engorde de los mejillones cultivados en Turpialito, estableció los períodos de máximo engorde de febrero a octubre y los mínimos de octubre a enero. Esto coincide con los resultados obtenidos y corroboraron el patrón de fluctuación del índice de engorde de los mejillones cultivados en el Golfo de Cariaco. Al tratar de explicarse las causas que originan estas fluctuaciones, señala que es imposible determinarlas con las observaciones obtenidas acerca de la fase del ambiente, ya que varios posibles agentes causantes pueden ocurrir simultáneamente.

El área de estudio se caracteriza por presentar dos períodos de productividad bien definidos: de finales de enero a agosto donde la surgencia mantiene altos niveles de productividad primaria y de septiembre a diciembre en donde los niveles de productividad declinan (Mandelli y Acuña, 1975). Estos niveles de productividad fueron relacionados con los vientos predominantes en el área. Durante el período de alta productividad predominaron las diatomeas, observándose un aumento considerable de febrero a abril. Los microflagelados predominan en el período julio-septiembre y los dinoflagelados presentan un máximo en agosto (Elvira Reyes, comunicación personal).

Como puede observarse, los períodos de mayor crecimiento coinciden con los períodos de mayor productividad y abundancia de organismos. Por otro lado, podemos hacer notar que también coinciden con los períodos donde el índice de engorde presenta valores altos. Es muy posible que la abundancia de estos organismos sea responsable de una mayor tasa de crecimiento. Los valores máximos del índice de engorde en los dos ciclos estudiados, están ubicados en agosto, lo cual concuerda con los resultados de Vélez (1971). Esto podría estar en relación con la gran abundancia de dinoflagelados y microflagelados presentes en el agua.

Se hace evidente que la tasa de crecimiento, así como el valor del índice de engorde, se reduce al mínimo en los meses de octubre a enero. Esto sugiere que el crecimiento y el engorde del mejillón, son afectados durante este período por la ocurrencia de fenómenos intrínsicos o extrínsicos. Entre los primeros podemos citar la pérdida de gametos y entre los segundos, la ausencia de alimento. Si los órganos sexuales del mejillón representan una elevada proporción del total de las partes blandas, es de esperar que la fluctuación del índice de engorde sea motivado por la formación y pérdida de gametos. La pérdida de gametos pudo haberse producido por reabsorción o desove. Y esto a su vez halla influido en el crecimiento.

Es importante señalar que los períodos de reducción del crecimiento y del índice de engorde se corresponden con los de menor abundancia de organismos.

De todo lo expuesto en el presente trabajo podemos concluir lo siguiente:

(a) en el ciclo anual, el incremento de la tasa de crecimiento es relativamente alta en los meses comprendidos de febrero a septiembre. Durante los meses de octubre a enero, este incremento es muy bajo;

(b) las fluctuaciones del índice de engorde para los dos años estudiados tienden a repetirse en años sucesivos y presentan características muy semejantes a las del crecimiento;

(c) los períodos de crecimiento y engorde aparentemente siguen las fluctuaciones en abundancia de los organismos fitoplanctónicos, y

(d) las tasas de crecimiento y engorde probablemente están asociadas con la reproducción o la ausencia de alimentos.

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JAMAICA SPINY LOBSTER INVESTIGATIONS

by

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1. INTRODUCTION
2. THE FISHERY FOR LOBSTER IN JAMAICA
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4. CONSERVATION
5. ACKNOWLEDGEMENTS
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Abstract

Spiny lobsters (*Panulirus argus*) from commercial fish trap catches along the south coast were examined from January, 1974 to March 1976. Studies were made on aspects of its biology and fishery dynamics, particularly reproduction, feeding, growth, population structure and conservation.

Resumen

Desde enero de 1974 hasta marzo de 1976 se han examinado las langostas (*Panulirus argus*) capturadas con nasa en las pesquerías comerciales de la costa meridional, estudiando diversos aspectos de su biología y dinámica pesquera, en especial reproducción, alimentación, crecimiento, estructura de la población y conservación.

1. INTRODUCTION

There is thought to be a decline in the landings of spiny lobsters, Panulirus argus, in Jamaica, over the last decade at least, at a rate which cannot be determined exactly due to lack of statistics. As a result the Fisheries Division undertook a small-scale investigation of the spiny lobster fishery, beginning January 1974. This paper presents results of work done from that time until March 1976. Spiny lobsters taken in trap catches along the south coast (Fig. 1) were examined on a regular basis. All traps were covered with 1¼ in (3.17 cm) hexagonal "chicken-wire" mesh which has a maximum aperture size of 4.13 cm.

2. THE FISHERY FOR LOBSTER IN JAMAICA

2.1 Species

The lobster fishery involves mainly the family Palinuridae. As in most parts of the Caribbean, the common spiny lobster Panulirus argus comprises almost 99 percent of the catch. A few specimens of P. guttatus (Latreille), the Guinea chick or chicken lobster, along with even fewer of Scyllarides aequinoctialis (Scyllaridae), the sand or slipper lobster, are also caught but are generally of little importance to the fishery. Rarely, specimens of Justitia longimana (Palinuridae) are reported captured in deep traps on the north coast.

3. BIOLOGICAL REPORT

3.1 Reproduction

3.1.1 Sexual maturity

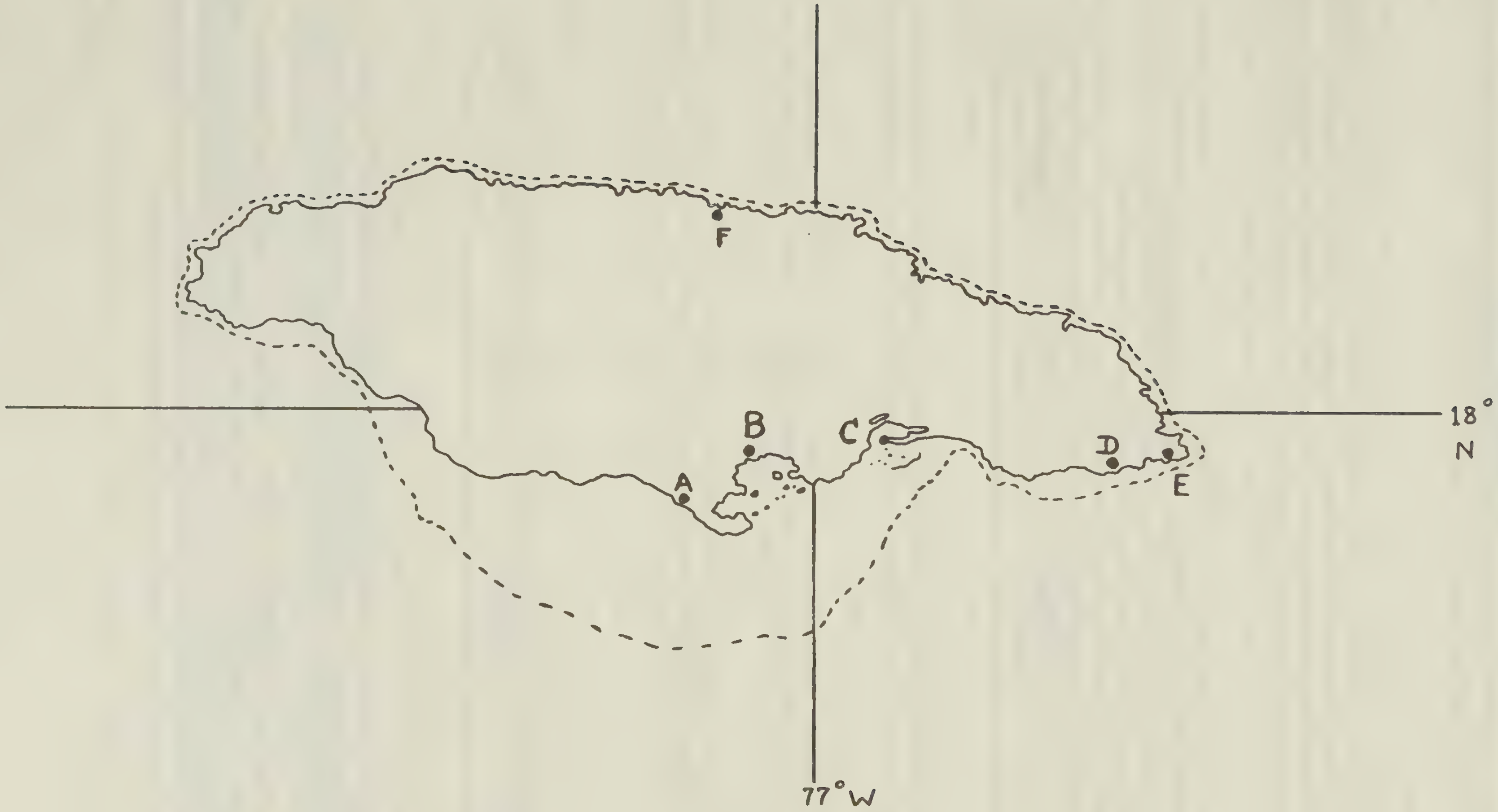
In this study the smallest egg-carrying female measured 73 mm carapace length (CL). Table I shows that females mature at 80 to 90 mm CL and the mean size at maturity is 90 mm CL.

TABLE I

Proportions of female Panulirus argus in successive size classes found bearing spermathecae or eggs; January 1974 to March 1976 (All specimens from trap catches in Jamaican waters)

Carapace length (cm)	Number examined	Number mature	Percentage mature
4.0-4.9	5	0	0
5.0-5.9	31	0	0
6.0-6.9	122	2	2
7.0-7.9	303	39	13
8.0-8.9	368	193	52
9.0-9.9	174	127	73
10.0-10.9	72	61	85
11.0-11.9	19	15	79
12.0-12.9	(7)	(5)	(71) [a]
TOTAL	1 101	442	

[a] Samples of less than 10 specimens are bracketed



Key: A – Rocky Point, Clarendon
B – Old Harbour Bay, St. Catherine
C – Port Royal, Kingston
D – Prospect, St. Thomas
E – Rocky Point, St. Thomas
F – St. Ann's Bay, St. Ann

Fig. 1 Map of Jamaica showing sampling sites and the 200 m contour line

Chittleborough (1974) observed that in P. longipes cygnus, the Western Australian rock lobster, the size at first maturity for the first captive specimens of Palinuridae successfully reared to maturity anywhere was 97-106 mm CL. He also mentioned that George (1958) found the mean size at first maturity was 76 mm CL in the wild.

3.1.2 Spawning seasons

Many investigators have reported on the seasonal occurrences of berried P. argus in the Western Atlantic and the Caribbean. The greatest frequency of berried females, according to Munro's 1974 review of Caribbean investigators, is "in the months from February to August". However, data collected during this study appear to indicate about two maxima of spawning. Table II shows that the first occurs in March and the second in June.

TABLE II

The proportions of egg-carrying female Panulirus argus observed in different months from January 1974 to March 1976 (All specimens from trap catches in Jamaican waters)

Month	No. of females examined	No. with eggs	Percentage with eggs
January	119	5	4
February	201	17	9
March	91	19	21
April	104	4	4
May	40	7	18
June	35	16	46
July	32	3	9
August	63	7	11
September	47	1	2
October	50	3	6
November	53	6	11
December	185	16	9
TOTAL	1 020	104	

3.2 Predation

During this study the spotted moray Gynothorax moringa was observed to prey on juvenile P. argus at the Port Royal reefs. Jamaican lobster vendors report that occasionally an octopus will feed on lobsters stored in crawls in shallow (1 metre) water near to shore.

Tiny (1 mm) goose barnacles (Lepas sp.) have been seen in substantial numbers on many occasions around the mouth appendages of all size ranges of lobsters during this study. In addition, barnacles (Balanus ebureus) have been seen on the dorsal carapace, sometimes along with encrustations of diatoms, algae and occasional bryozoans and, as stated by Buesa Mas (1965), could serve as indicators of habitat and the intermoult period.

On one occasion a 97 mm CL male P. argus was observed with a 2-cm diameter wound scar in the lower left lateral carapace just above the leg bases. This appeared to have been caused by a speargun and, further, it is thought at least one moult had occurred since the wounding.

On several occasions female P. argus were observed with the telson area severely abraded and shredded.

3.3 Nutrition and Growth

3.3.1 Feeding and food

The spiny lobster will take a wide range of food; examination of stomach contents shows small molluscs such as young conchs (Strombus sp.) gastropods, clams and occasionally young lobsters (Walton Smith, 1959).

During feeding studies with P. argus juveniles and sub-adults in aquaria at the Fisheries Division small specimens of the following intertidal gastropod molluscs were eaten: Crassispira nigrescens, Nerita tesellata, Littorina angulifera, Diadora sp. and Tegula excavata.

3.3.2 Age and growth

As length-frequency histograms compiled from data gathered during the present study displayed stationary modes, it was not possible to make an estimate of an absolute growth rate.

A 75-mm female in captivity took 113 days to moult during this study; it is thought this period was unusually long. Three juvenile male P. argus ranging in size from 25 to 28 mm CL, took 12, 50 and 51 days respectively to moult.

According to Peacock (1974) Antiguan and Barbudian P. argus from 60-90 mm CL have calculated ages of "1.5 to 2 years". The average size range of P. argus examined from all sources (both sexes) ranged from 50-120 mm CL; thus the estimated ages of these Jamaican specimens ranged from just over 1 year to about 3 years.

3.4 Behaviour

During this study, aquarium observations were made on P. argus sub-adults, particularly aspects of feeding, territoriality and aggression, over a four-month period. (Aquaria measured 120 x 34 x 45 cm.)

In general, observations on the formation of a "pecking order" (hierarchy) were similar to those noted of Strangways-Dixon, in Munro (1974) and Squires (pers. comm.), where the largest specimen inhabits the most favourable shelter.

On several occasions during these investigations it was noted there was an increase in lobster landings after the passage of bad weather. It is not known whether or not this was related to increased feeding activity after weather-induced turbulence.

3.5 Population Structure

3.5.1 Sex ratios

Sampling revealed that the sex ratio of those populations sampled remained generally close to unity.

3.5.2 Size composition

Fig. 2 shows the monthly composition of male and female P. argus examined at Port Royal fishing beach taken from trap catches during the period August 1974 to October 1975.

Mean lengths of males and females landed at Port Royal from August 1974 to October 1975 were 83.7 mm and 79.4 mm CL respectively. These came from relatively exploited reefs around southern Jamaica.

Fig. 3 shows the size composition of P. argus of both sexes in samples of trap catches landed at Old Harbour Bay beach, St. Catherine. (I) shows the distribution of those sampled from January to June, 1974 and (II) those sampled from June to October 1975 as cumulative carapace length-frequency histograms. Mean lengths of those males and females shown in I were 65.3 mm and 62.4 mm CL respectively. Mean lengths for males and females in II were 75.2 and 73.4 mm CL respectively.

Fig. 4A shows the carapace length-frequency histograms of trap catches sampled from May to November 1974 at Rocky Point, Clarendon. Mean lengths of recruited stock were 80.1 mm and 75.2 mm CL for males and females respectively.

Fig. 4B illustrates the cumulative carapace length-frequency distribution of P. argus of both sexes landed at Port Royal. Although the mean lengths of recruited males and females differ by only 4.3 mm CL, examination shows that males have a relatively greater proportion (45.3 percent) of specimens larger than the common modal length of 80.0-89.0 mm CL than do the females (28.8 percent).

Four P. argus were examined at Rocky Point, St. Thomas, (4.13 cm mesh) landed from trap catches. Three females had a mean length of 81.3 mm CL while the male was 116.0 mm CL.

At Prospect, St. Thomas, four females from a spear-fisherman's catch were examined; mean length was 89.0 mm CL.

During the present study, calculations of the relative abundance of successive length groups were made and are shown in Table III. There are rapid declines in abundance at sizes exceeding those at full recruitment for both sexes. It is thought that these rapid declines are a result of the intensive trap fishery.

3.6 Recruitment

From the available data, male and female P. argus appear to become fully recruited to the trap fishery which lands its catch at Port Royal; this is at 80.0-89.0 mm CL. This estimate is based on a much larger sample size than Munro's which gave the same value.

This value is 20 mm CL smaller than Peacock's (1974) estimate for the Barbudian offshore trap (4.13 cm mesh) fishery and 10 mm CL more than his estimate for the diving fishery there.

From available data on the Old Harbour Bay trap fishery, both sexes appear to become fully recruited to that fishery at about 70 mm CL. Estimates of sizes at full recruitment for P. argus landed at Rocky Point (Clarendon) are 80-89 and 70-79 mm CL for males and females respectively.

P. argus less than 40 mm CL were not encountered during the present investigations and 40 mm CL appears to be the minimum retainable length for traps of 4.13 cm mesh as used in the south coast Jamaican fishery.

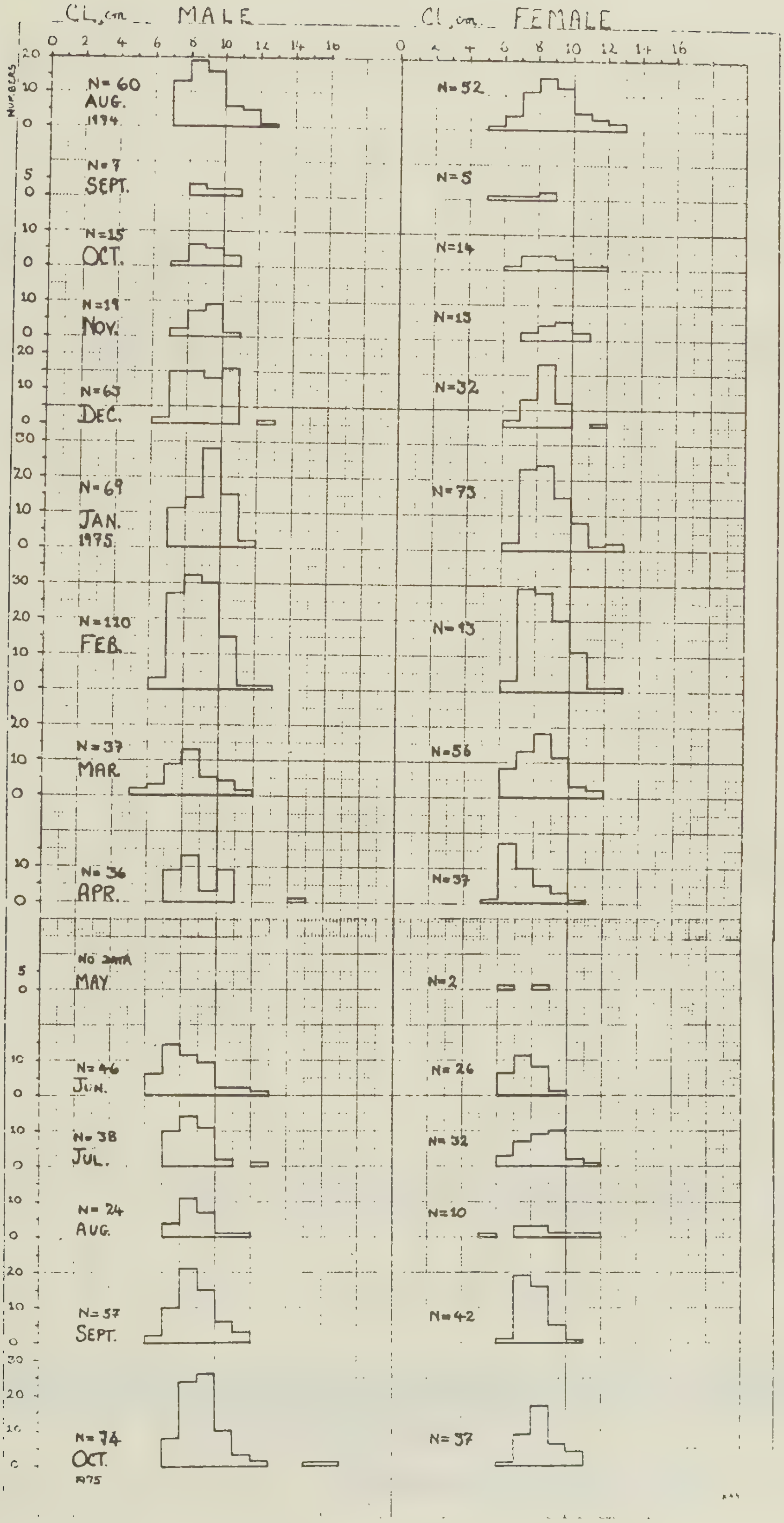


Fig. 2 Carapace length-frequency histograms of samples of P. argus landed at Port Royal, Kingston from August 1974 to October 1975

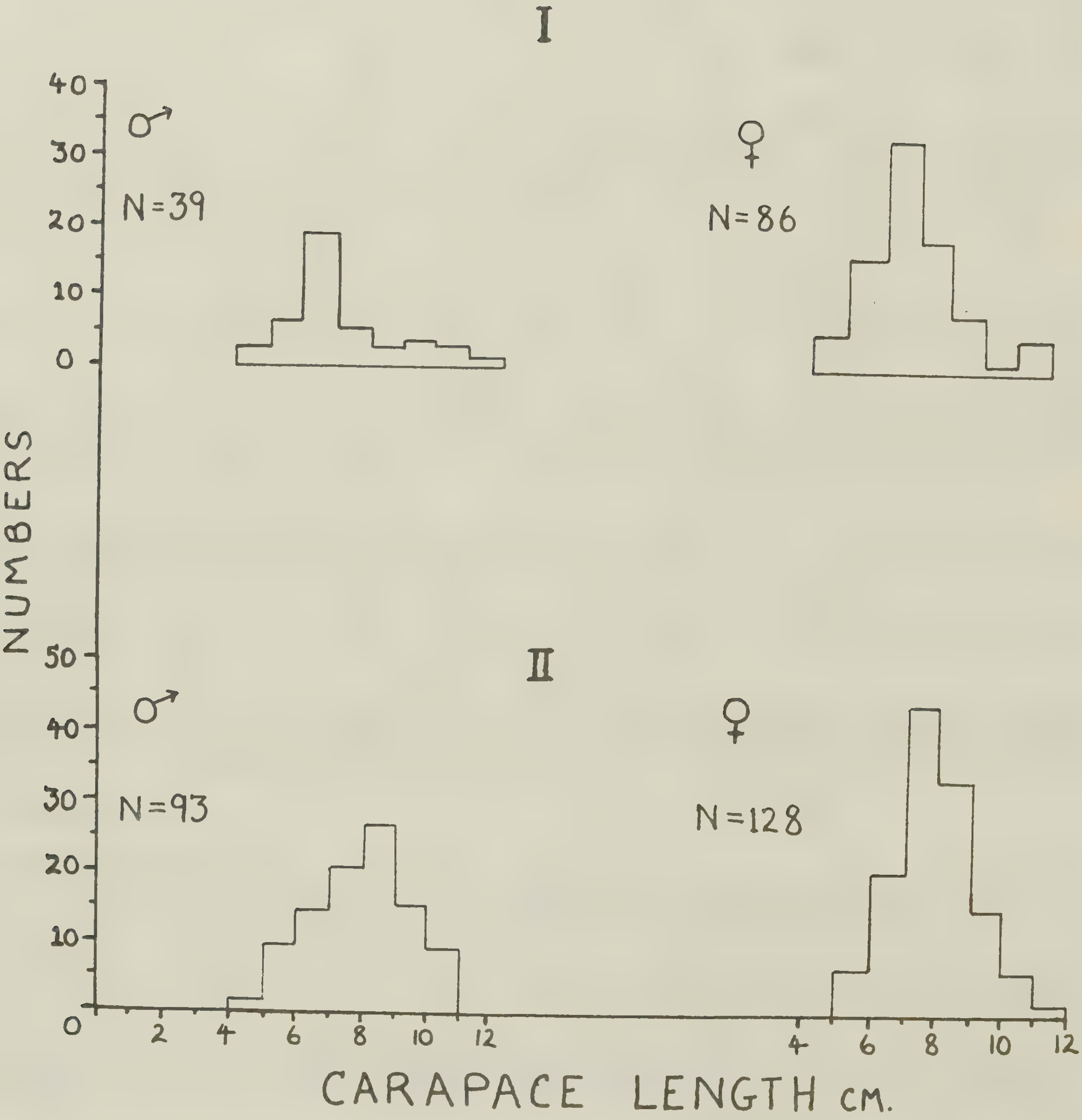


Fig. 3 I Cumulative carapace length-frequency histograms of samples of P. argus landed at Old Harbour Bay, St. Catherine, January to June 1974

II June to October 1975

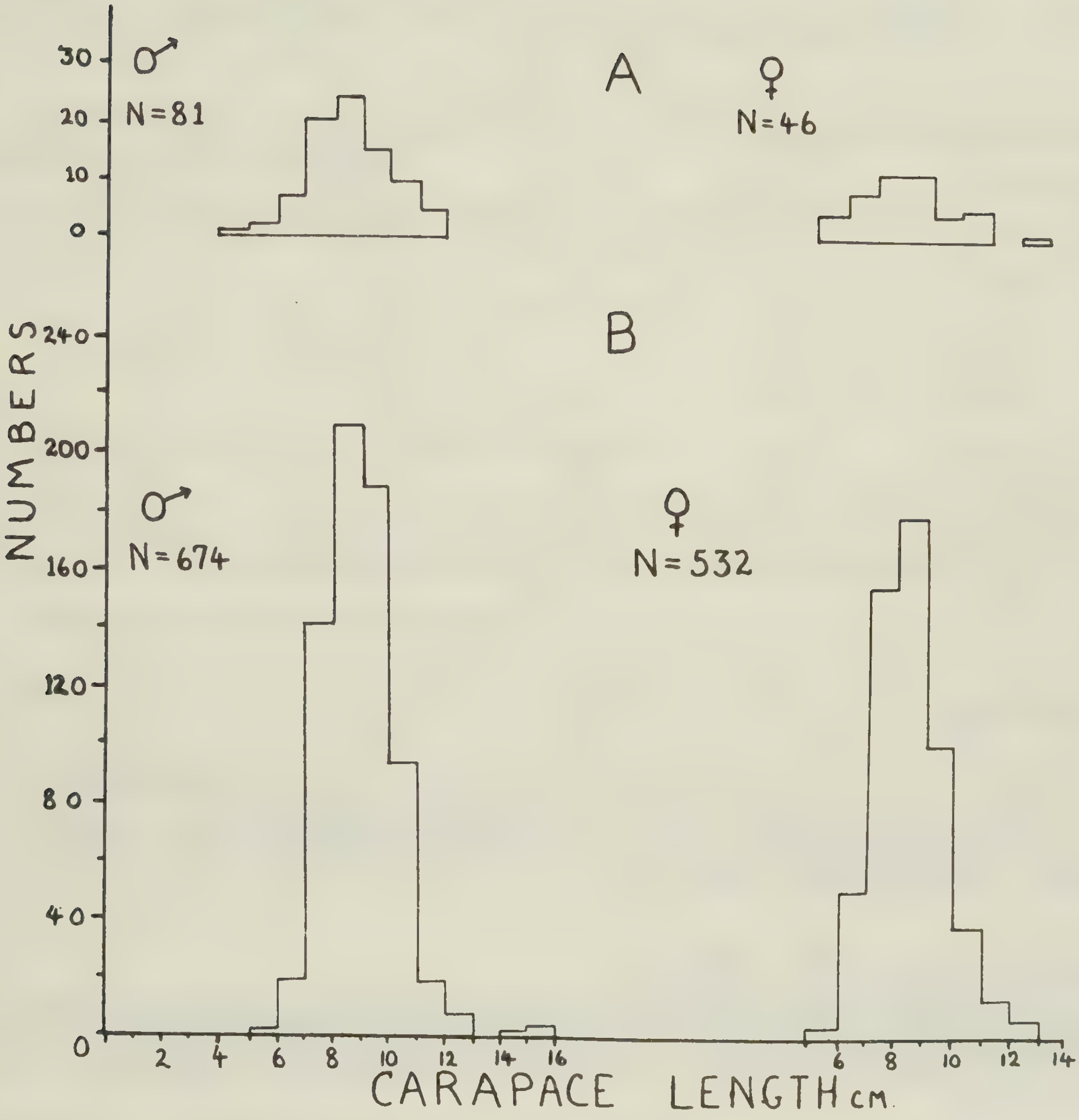


Fig. 4 A. Cumulative length-frequency histograms of samples of P. argus landed at Rocky Point, Clarendon, from May to November 1974

B. Port Royal, August 1974 to October 1975

TABLE III

Relative abundance of successive length groups of male and female *Panulirus argus* landed at Port Royal from commerical trap catches
(All catches from south coastal waters, August 1974 to March 1975)

Length group	Males % frequency in catch	Relative abundance	Females % frequency in catch	Relative abundance
5.0-5.9	0		0.7	
6.0-6.9	1.7		4.5	
7.0-7.9	21.3		27.4	
8.0-8.9	27.6		33.2	1.00
9.0-9.9	30.4	1.00	20.9	.63
10.0-10.9	16.0	.53	8.9	.27
11.0-11.9	2.2	.07	2.7	.08
12.0-12.9	0.8	.03	1.7	.05
Mean CL of recruited stock = 85 mm		Mean CL of recruited stock = 82 mm		

4. CONSERVATION

Briefly, the urgent need for conservation is shown by the fact that 76 percent of the total commercial south coast female lobster catch examined during this study consisted of immature females, i.e., less than 90 mm CL. Florida's spiny lobster fishery is considered to be still in need of conservation with 17-21 percent of the total commercial harvest consisting of immature females (Davis, 1974).

4.1 Minimum Size Conservation Regulations

Munro (1974) extensively reviewed local spiny lobster fishery dynamics with reference to conservation. He stated, "In addition to questions relating to gross yield per recruit...... several factors require consideration in arriving at a suitable minimum size". He went on to state in part that:

1. The mean size at maturity of females (about 95 mm CL) should represent the lowest acceptable limit.

2. A minimum size of at least 110 mm CL would appear to be the most suitable for the south coast and that "even larger minimum size would be indicated" for all other areas.

3. That an islandwide minimum size of 108 mm ($4\frac{1}{2}$ in) carapace length would be theoretically the most realistic one.

The main point in Munro's argument was "any restraint on the harvesting of small sizes of P. argus will result in substantial increases in yield" and this indeed is the whole point of enforcing a minimum size regulation.

However, the size he recommended on theoretical grounds (108 mm CL) is, in the context of the socio-economic consequences of earning losses to fishermen and vendors, too high as a first or initial size limit.

From observations made during this study, a more practical initial minimum size of 70 mm (2 3/4 in) CL is therefore recommended. This size, it is thought, will produce far less adverse socio-economic repercussions.

It should be made clear at this point that this minimum size limit is to be modified upwards at intervals. The rough sequence to be followed is set out below.

1976 - 70 mm (2 3/4 in) Carapace length
1978 - 76 mm (3 in) CL
1980 - 80 mm (3¼ in) CL
1985 - 85 mm (3 3/8 in) CL

4.2 Protection of Egg-carrying ("Berried") Females

Briefly, it is felt that egg-carrying female P. argus must be protected by legislation requiring their return to the sea and prohibiting their sale. The main reason for this is although the calculated average fecundity of a mature female is about 800 eggs per gram body weight (Munro, 1974) over 99 percent of these die after release by the female.

4.3 Protection of Soft-shelled Individuals

This relates to the conservation of those P. argus which have moulted and their exoskeletons have not yet completely hardened. It is felt that these must be protected also. Their market value is nil, or nearly so, in most cases; these may not be taken in Belize.

5. ACKNOWLEDGEMENTS

Mr. Nelson Miller (Fisheries Instructor) assisted with data collection from December 1974. Acknowledgement is also made to E.L. Hamblyn and R. Sanhueza and to the U.W.I. Port Royal Marine Laboratory.

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EPIPHYTISM AND ANTIBIOTIC ACTIVITY OF EXTRACTS OF TROPICAL MARINE ALGAE

by

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CONTENTS

1. INTRODUCTION
2. METHODS AND MATERIALS
3. RESULTS AND DISCUSSION
4. ACKNOWLEDGEMENTS
5. REFERENCES

Abstract

For a two-year period, offshore algae from La Parguera, Puerto Rico, have been examined for epiphytic flora. One hundred and nine species of epiphytic algae have been identified, which represent 60.5 percent of the total number of algae found in the area. Algal hosts varied considerably in their suitability to support epiphytes, although on most hosts epiphytism was heaviest on older portions.

Antibiosis was observed in several host plants, and its possible ecological importance affecting epiphytism was examined. Antibiotic activity against sensitive marine bacteria was generally at a maximum near the growing tips and decreased with distance from the apical areas. Preliminary results, however, showed that bacteria isolated from basal non-antibiotic portions of an alga were not sensitive to the antibiotic properties of apical portions of the same plant. Patterns of epiphytes on different hosts appear not to be influenced by host antibiosis.

Resumen

Durante dos años se ha examinado la flora epifítica de las algas que se encuentran frente a La Parguera, Puerto Rico, individuando 109 especies de algas epifíticas, que representan el 60,5 por ciento del número total de algas que se encuentran en esa zona. Se han registrado notables diferencias en la capacidad de las algas hospedantes de sustentar epifitos, aunque en casi todas ellas se observó un epifitismo más intenso en las partes más viejas de la planta.

En varias algas hospedantes se observó antibiosis, y se examinó su posible importancia ecológica en relación con el epifitismo. La actividad antibiótica contra las bacterias marinas sensibles resulta en general mayor cerca de los extremos, donde la planta crece, disminuyendo a medida que aumenta la distancia de las zonas apicales. Sin embargo, los primeros resultados muestran que las bacterias aisladas en partes basales no antibióticas de un alga no son sensibles a las propiedades antibióticas de las partes apicales de la misma planta. No parece que en el epifitismo de distintos hospedantes influya la antibiosis de éstos.

1. INTRODUCTION

During the past several years, an offshore algal flora has been studied with special reference to epiphytic algae. Epiphytes are plants that live on other plants. Due to their frequently small size, numerous epiphytic species can be easily overlooked in taxonomic accounts of various algal floras. Nevertheless, epiphytes may comprise a large portion of the algal species present within a particular area (Humm, 1964; Ballantine and Humm, 1970).

By definition, epiphytes utilize their hosts for substrate and do not receive nutrients from them. Several studies, however, have shown that isotopically labelled substances can move from host to epiphyte and *vice versa*, indicating that the relationship is not always static (Ende van Den and van Oorschot, 1963; Linskens, 1963a; Harlin, 1973). This type of inter-relationship might be responsible for some reported examples of host-epiphyte specificity (Harlin, 1971; Citharel, 1972). The discovery that many algae possess antibacterial properties (see reviews by Burkholder and Sharma, 1969; Sieburth, 1964) has raised some interesting speculation regarding the ability of some plants to exert a controlling influence over which organisms may grow on the plant surface. Conover and Sieburth (1964) and Sieburth and Conover (1965) suggest that epiphyte zonation on *Sargassum natans* as well as on *Ascophyllum nodosum* (Sieburth *et al.*, 1974) could be a result of "antifouling" substances produced by hosts. Sieburth *et al.* (1974) speculate that the production of "antifouling" substances might be a characteristic of marine plants in general.

The present study is an attempt to evaluate the possible role of algal antibiosis as it affects organisms that colonize its surface.

2. METHODS AND MATERIALS

Algae were collected from an area located two miles south of La Parguera, Puerto Rico, in 55 ft of water. Collections were made by dredging from the RV MEDUSA and SCUBA diving. Host plants were sorted by species, preserved and later examined for their epiphytic flora. All epiphytic species were recorded for the different hosts on which they were found.

2.1 Antibiosis Experiments

Antibiotic activity of different hosts was measured using the disc method as described by Burkholder *et al.* (1962) and Almodóvar (1964) with the exception that fresh material was used. Inhibition was measured in millimetres of the clear area from the edge of the disc to the inner margin of the surrounding bacterial growth. As assay organisms, two sensitive marine bacteria were obtained from cultures isolated from seawater by Dr. Paul Burkholder (numbers 13 and 213). A third species (number 20) was also isolated from mud in shallow water at Magueyes Island, marine facility for the Department of Marine Sciences, University of Puerto Rico. The bacteria were maintained on Bio Cert nutrient seawater agar (1.5 %).

2.2 Algae - Bacteria Experiments

Bacteria were isolated from apical segments of *Halimeda opuntia*, previously determined to be antibiotic, and from basal segments which were shown to lack antibiosis or with reduced activity. Segments were rinsed in sterile seawater to remove loosely associated bacteria, placed in flasks containing 10 ml liquid media and then incubated for 6 h in light in a shaker culture. Agar plates were then streaked and replated until pure cultures were obtained Bacteria were also isolated from *Dictyopteris delicatula* following the same procedure. An enriched seawater medium containing 2 g peptone, 2 g trypticase, 1 g yeast extract and 1 microgram vitamin B_{12} per litre of seawater (Burkholder, unpublished) was utilized in these isolations.

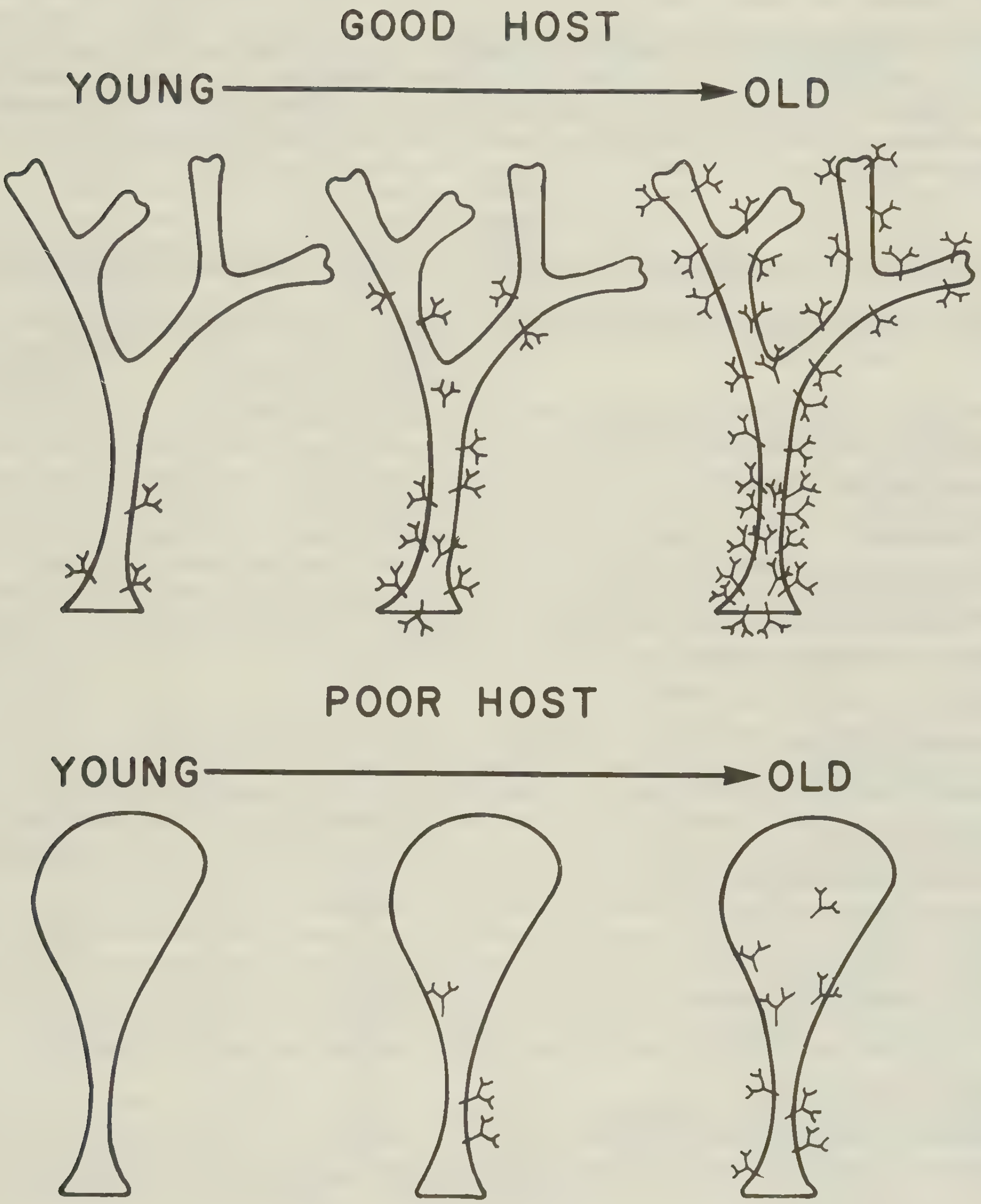
GOOD HOST
YOUNG
OLD
POOR HOST
YOUNG
OLD

Fig. 1 Diagrammatic illustration of epiphyte zonation on good andpoor hosts and changes with age

3. RESULTS AND DISCUSSION

One hundred and nine species of epiphytes were identified which represents 60.5% of the total offshore flora examined. After examining a variety of hosts, it was apparent that these plants varied considerably in their suitability to support epiphytes. Table I presents data on numbers of epiphytes identified on selected hosts during the study period. Some hosts, including *Bryothamnion triquetrum*, *Laurencia poitei* and *Digenia simplex*, generally supported an abundance of epiphytes. It was not uncommon to find as many as 20 epiphytic species on an individual "good" host. The 62 species of epiphytes found on *Bryothamnion* represent over half the total epiphytic flora identified. Probably most epiphytic species are capable of living on these good hosts. The fact that more species have not been recorded could reflect insufficient collecting.

TABLE I

Numbers of epiphyte species found on different algal and seagrass hosts

Host Algae	Average Number Epiphytes/Collection	Total Epiphytes Identified
Bryothamnion triquetrum (Rhod.)	15.8	62
Laurencia poitei (Rhod.)	16.3	56
Digenia simplex (Rhod.)	13.2	56
Dictyota dichotoma (Phae.)	11.8	45
Sargassum ramifolium (Phae.)	16.8	44
Gracilaria compressa (Rhod.)	12.0	39
Acanthophora spicifera (Rhod.)	10.0	37
Lobophora variegata (Phae.)	8.0	36
Codium isthmocladum (Chlor.)	7.9	30
Anadyomene stellata (Chlor.)	5.6	29
Hypoglossum tenuifolium (Rhod.)	4.5	22
Agardhiella tenera (Rhod.)	8.5	21
Spyridia aculeata (Rhod.)	7.3	18
Halophila baillonis (Angio.)	4.6	18
Dasya pedicillata (Rhod.)	3.5	14
Halymenia floresia (Rhod.)	3.1	14
Chrysymenia enteromorpha (Rhod.)	2.5	6

Chlor. = Chlorophyta
Phae. = Phaeophyta
Rhod. = Rhodophyta
Angio. = Angiosperm

Other hosts ("poor") supported far fewer epiphytes. Large plants of Dasya pedicillata, Halymenia floresia and Chrysymenia enteromorpha frequently were entirely devoid of epiphytes. When present, epiphytes were generally limited to few individuals comprising just a few species. Never more than three species of epiphytes were found on any individuals of Chrysymenia.

On almost all hosts a general zonation pattern of epiphytes was observed. Generally, epiphytism was heaviest in the older portions of the plant. Both abundance of epiphytes and numbers of species decreased with proximity to apical areas. This zonation is frequently striking. The suitability of algal hosts to support epiphytes also changes with age of the host. Fig. 1 represents this change diagrammatically. In this illustration, as is the case with most of the hosts examined, the uppermost portion is the apical growing area and is the youngest part of the plant, while the basal area is the oldest. On all algal hosts, epiphytes increase in both abundance and number of species with age of host. On good hosts, epiphytes are found distributed closer to the apical tips, although colonization is still heaviest on older portions. Epiphytes may eventually completely cover an old host, obscuring the distribution pattern. Poor hosts also become more suitable with age; however, as mentioned above, numbers of epiphytes are reduced.

Conover and Sieburth (1964) found a zonation of epiphytes on Sargassum natans and S. fluitans similar to that described above. On these hosts, portions of the plant devoid of epiphytes produced substances which inhibited the growth of sensitive bacteria, while older portions (with epiphytes) no longer produced these substances. In an attempt to determine if the host plant were somehow regulating its epiphytic flora, a number of algae of known host suitability were screened for their antibiotic activity. If antibiosis were a mechanism related to, or responsible for, the lack of epiphytes on some hosts and the general zonation pattern of epiphytes, one would expect a correlation between the presence of antibiosis in a plant or plant part and the absence of epiphytes on poor hosts and in apical growing areas.

Of a total of 38 algae tested, 10 showed some antibiotic activity. The degree of antibiosis was not constant, being variable at different times when tested for the same plant. The activity was generally greater for apical areas than basal when antibiotic. Table II lists some of the algae examined. Among the good hosts, antibiotic activity was detected only on Dictyota dichotoma, (3.6.75) and this was not repeatable. Chrysymenia enteromorpha was the only poor host displaying antibiosis. This was not great, amounting to an inhibition of only 1 mm. Almodóvar (1964) demonstrated that antibiosis in Halimeda opuntia was generally greatest during winter months and least during summer. Comparable fluctuations observed in this study were not accompanied by obvious changes in epiphytism on Halimeda. Asparagopsis taxiformis displayed the greatest antibiotic activity. Upper apical portions of this alga were, usually, completely devoid of epiphytes, while the lower areas of some were colonized by epiphytes. This growth of epiphytes was found despite considerable antibiotic activity.

There was no obvious correlation between epiphytic patterns and algal antibiosis in the cases examined. These results do not support the idea that antibiosis is important in regulating epiphytism. Berland et al. (1972) caution about use of the disc method in the evaluation of antibiosis; substances are released in grinding that, under normal conditions, might not be liberated.

A number of earlier reports on algal antibiosis were made utilizing terrestrial pathogens as assay bacteria in an assessment of potential pharmaceutical value of algal products. In some of these studies, a number of algae have been labelled antibiotic, including the good host Digenia simplex (Katayama, 1962); they were not found to be active by the procedures employed here. Tests with marine bacteria seem more relevant; it is hard to imagine the adaptive value to marine algae of the capability to synthesize products which inhibit terrestrial bacteria.

TABLE II

Antibiotic activity in some selected marine algae

				Assay Bacteria[a]		
Alga	Date	Coll. Site	Plant Portion	13	213	20
Acanthophora spicifera	3.6.75	2	apical	0	0	0
Anadyomene stellata	9.7.75	1	apical	0	0	0
	5.9.75	1	apical	0	0	0.5
Asparagopsis taxiformis	26.3.76	1	apical	4	6	7
			basal	5	5	9
	27.5.76	1	apical	4.5	6	7
			basal	2	3	3
Bryothamnion triquetrum	3.6.75	2	apical	0	0	0
Chrysymenia enteromorpha	9.7.75	1	apical	1	1	T
Dasya pedicillata	26.3.76	1	apical	0	0	0
Dictyopteris delicatula	3.6.75	2	apical	8	4	4
	8.1.76	2	apical	0	0	0
Dictyota dichotoma	3.6.75	2	apical	0	T	0
	9.7.75	1	apical	0	0	0
Digenia simplex	9.7.75	1	apical	0	0	0
Gracilaria compressa	3.6.75	2	apical	0	0	0
Halimeda opuntia	26.3.75	3	apical	4.5	6	5.5
			basal	0	3	1
	23.9.75	3	apical	0	2	2
			basal	0	0.5	0
Halophila baillonis	9.7.75	1	apical	0	0	0
Halymenia floresia	5.9.75	1	apical	0	0	0
Hypoglossum tenuifolium	9.7.75	1	apical	0	0	0
Laurencia poitei	9.7.75	1	apical	0	0	0
Lobophora variegata	9.7.75	1	apical	0	0	0
Scinaia complanata	26.3.76	1	apical	0	0	0

[a] Inhibition measured in millimetres; T = trace

Collection sites:
1. Media Luna Reef (55 ft)
2. Ballena Bay (2-6 ft)
3. Enrique Reef (1-2 ft)

Some theories regarding lack of epiphytes on certain hosts include the reports of Linskens (1963) and Goodward (1934). Linskens felt that differences in the surface tensions of different hosts caused the variation in suitability of the host. Goodward reported that the heavy gelatinous surface of some algae is responsible for lack of epiphytes. Scinaia, Chrysymenia and Halymenia are poor hosts that are also extremely gelatinous. This surface may be physically unsuitable for attachment and germination of some algal spores. The simplest, and probably the best, explanation for zonation patterns of epiphytes on a given host is the difference in age between portions of a plant. Humm (1964) and Sieburth (1968) reported that the heaviest growth of epiphytes was generally on the oldest portions of seagrasses and marine algae. Settling of spores is a chance event. The upper, little colonized, portions have not been exposed so long as the older portions and therefore have had less time to develop an epiphytic community.

Bacteria are generally thought to be important colonizers in the succession of organisms on submerged surfaces (Zobell and Allen, 1935; Corpe, 1972), including algal surfaces (Conover and Sieburth, 1964). Thus, it was of interest to begin an examination of the bacterial flora found on antibiotic plants. Theoretically one might expect to find fewer bacterial species on an antibiotic apical thallus than elsewhere on the same plant, where antibiotic activity is reduced or absent. For example, the sensitive marine bacteria used here as assay organisms would not be expected to be present on an antibiotic portion of a plant.

Bacteria were differentiated on the basis of gross morphology. Four bacterial species were easily identified from Halimeda apical segments and six species were isolated from basal segments. Three species were probably common to both apical and basal portions, while the remaining three species from basal segments were pigmented forms not found on apical areas.

The bacteria obtained from Halimeda opuntia and Dictyopteris delicatula were used in an assay against apical (antibiotic) and basal (non-antibiotic) preparations of the plant from which they were isolated. As expected, all bacteria from apical portions of the plants were able to grow in the presence of the above preparations. None of the bacteria isolated from the non-antibiotic portions was inhibited by extracts of the apical (antibiotic) portions of the same plant. The difference observed in the bacterial flora between apical and basal Halimeda segments is probably due to the difference in age of the segments and not to antibiotic properties of the plant. While the number of bacterial species dealt with here is small, these results suggest antibiosis to have less of an ecological importance in tropical marine macrophytes than previously speculated.

4. ACKNOWLEDGEMENTS

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THE PATTERNED MIGRATION OF SHRIMP POPULATIONS: A COMPLETE STUDY OF CRANGON CRANGON AND PENAEUS BRASILIENSIS

by

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Abstract

In three previous papers on the biology of the western European brown shrimp (*Crangon crangon*), a method has been described to demonstrate the rigid patterns in migration and distribution of this species. The sensitiveness to stimuli triggering migration of brown shrimps depends on: the sexual category (berried females are more sensitive than non-berried females) and also on the physiological condition of the individual shrimps within these categories. The physiological condition is measured indirectly by defining the phase of the moulting cycle. Shrimps (Crangonidae and Penaeidae) increase in length between two consecutive moults by stretching the elastic parts of the carapace. Since the body length increases while the hard parts of the carapace do not, the relation between the surface area of certain shields of the carapace (SA) and the body length shifts during the intermoult. This shift makes it possible to define the phase within the intermoult in which the shrimps are. It was found that the sensitiveness to stimuli triggering migration decreases the farther the shrimp is away from the next moult. Among different waves of migrating shrimps a high measure of synchronization could be demonstrated in respect to the moulting cycle.

The same method has been applied to specimens of *Penaeus brasiliensis* trying to migrate from a salt water pond in the northeast of Brazil. The results obtained show a striking similarity to the migration pattern of *Crangon crangon* in the North Sea, suggesting strongly the existence of comparable rigid migration and distribution patterns in this penaeid.

Resumen

En tres trabajos anteriores sobre la biología del camarón pardo del oeste de Europa (Crangon crangon) se ha descrito un método para demostrar que los movimientos migratorios y la distribución de esta especie siguen un modelo rigido. La sensibilidad de estos camarones a los estímulos que determinan los movimientos migratorios depende del estado sexual de los camarones (las hembras con huevas son más sensibles que las sin huevas) y, aparte de eso, del estado fisiológico de cada camarón, que se mide indirectamente definiendo la fase en que se encuentra del ciclo de muda. Los camarones (Crangonidae y Penaeidae) aumentan de talla entre dos mudas consecutivas, estirando las partes elásticas del cutículo. Como la talla corporal aumenta y las partes duras del cutículo no lo hacen, la relación entre la superficie de algunos escudetes del cutículo y la talla del cuerpo varía durante el período comprendido entre las mudas. Este cambio hace posible definir la fase en que se encuentran los camarones en el período entre una muda y otra. Se ha hallado que la sensibilidad a los estímulos que determinan los movimientos migratorios es menos cuanto más falta para la muda siguiente. En grupos sucesivos de camarones en migración se halló un elevado sincronismo en el ciclo de muda.

El mismo método se ha aplicado a ejemplares de Penaeus brasiliensis que trataba de emigrar de un estanque de agua salada en el nordeste del Brasil. Los resultados obtenidos muestran una sorprendente similaridad con el modelo de migración de Crangon crangon en el Mar del Norte, lo que sugiere la existencia de modelos rígidos análogos de migración y distribución en este peneido.

1. INTRODUCTION

In three papers, Boddeke (1975, 1975a and 1976), a description was given of the seasonal migration of Crangon crangon, a common western European shrimp species (Fig. 1). From this work it has become evident that the autumn migration is a strictly patterned process in which successive waves of shrimps, both males and berried and non-berried females (of which categories the length composition is practically constant) move from inshore waters out to sea during normal winters.

This autumn migration is triggered by fluctuations of water-temperature, particularly those in the inter-tidal zone, resulting from the seasonal air and water temperature differences. The constancy of the composition of the waves of migrating shrimps, during virtually all the migrating period, suggests that the sensitivity to migration-triggering stimuli depends on the physiological condition of individual shrimps within the mentioned categories.

To measure the physiological condition of individual shrimps a method was used, developed originally to establish the growth of berried females during summer, based on growth between the moults. Considering the fact that in the life cycle of C. crangon very important physiological processes such as growth (Meixner, 1969), spawning (Tiews, 1954) and sex change, with respect to external characteristics (Boddeke, 1966), are coupled with moulting, we may conclude that the stage of the moulting cycle will give some indication of the physiological condition of an individual shrimp. For this reason, the "biological distance" to the next moult of adult female shrimps (berried and non-berried) has been used as a parameter for the individual physiological condition and the sensitivity to migration-triggering stimuli. With this "SA-L method" (see 2.2) the patterned character of the seasonal migration of C. crangon could be demonstrated clearly in the western Wadden Sea (Fig. 2; cf. Boddeke, 1975).

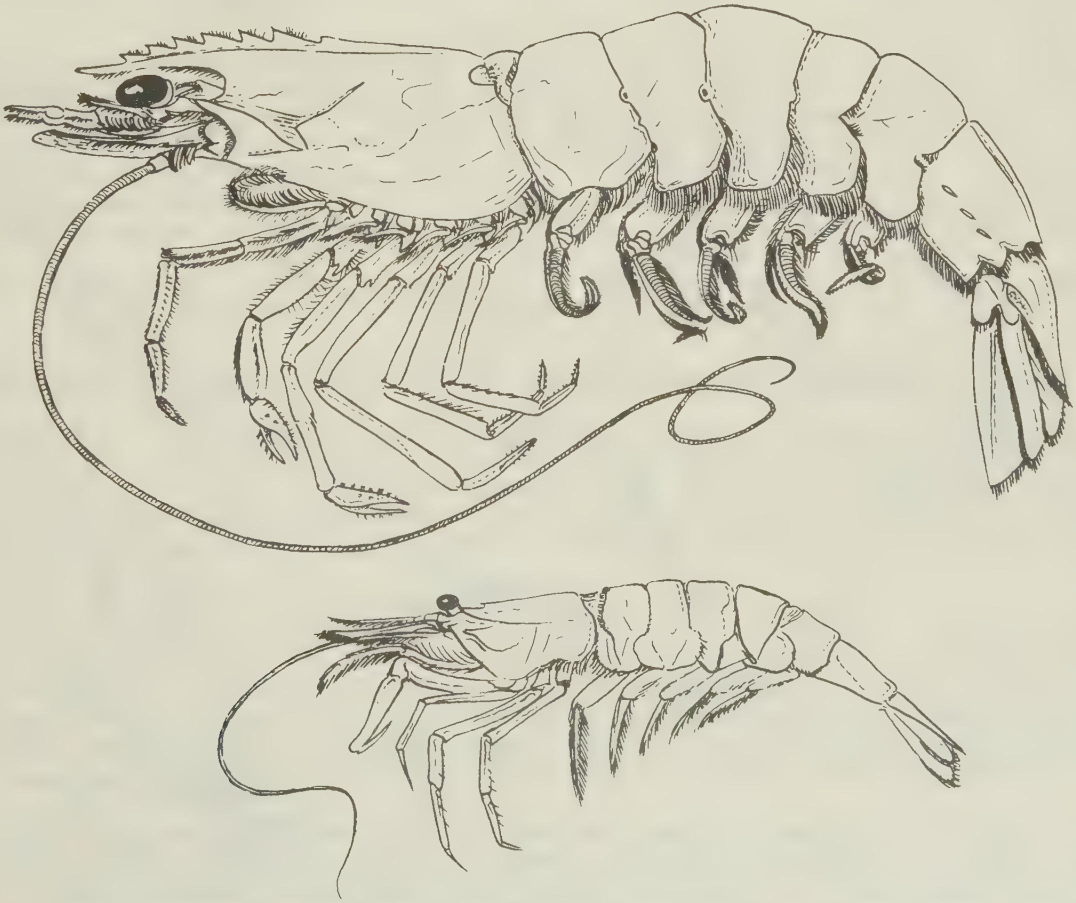
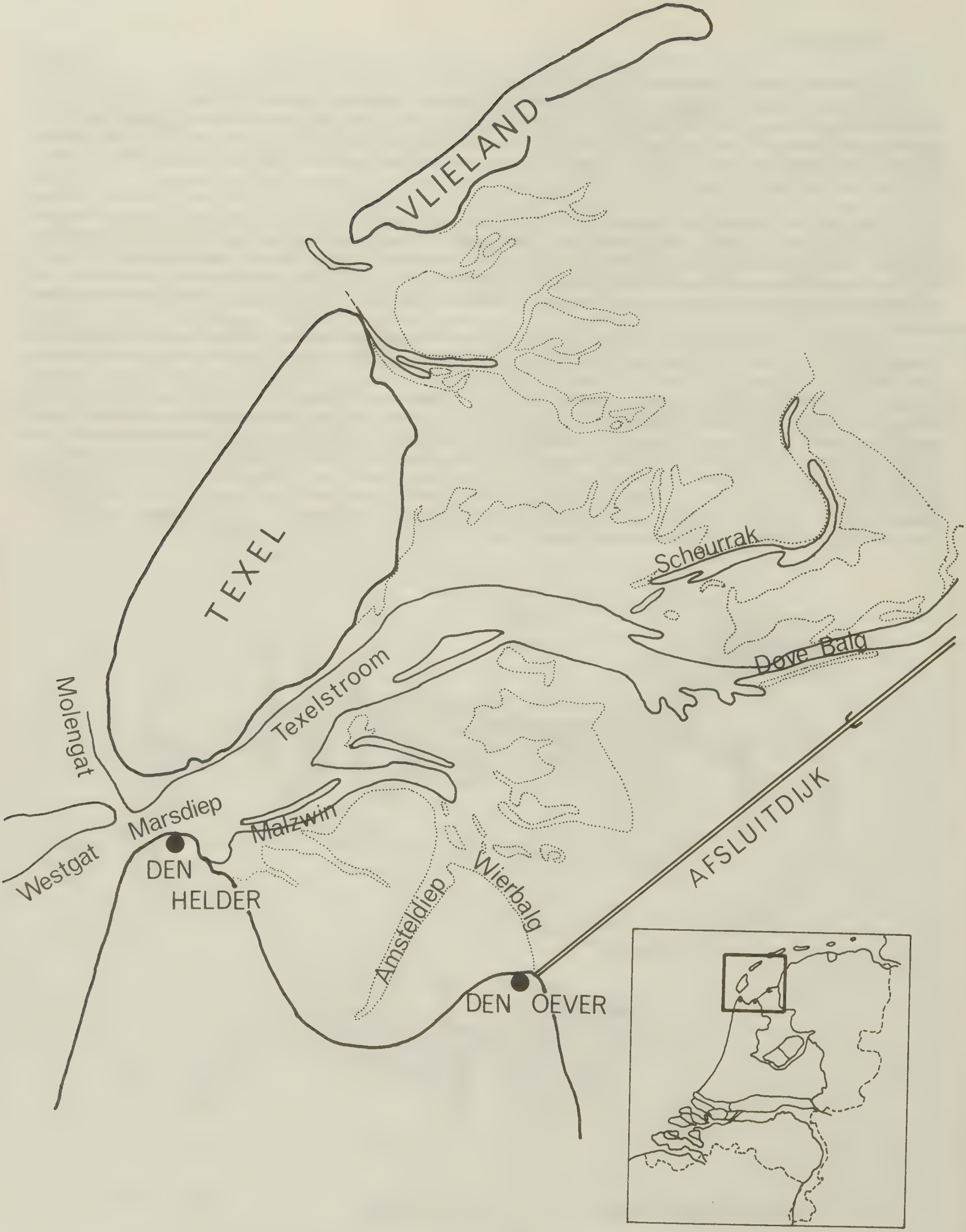


Fig. 1 Penaeus brasiliensis (top) and Crangon crangon. Adult specimens, both X 1.2


VLIELAND
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Westgat
Malzwin
DEN
HELDER
Amsteldiep
Wierbalg
AFSLUITDIJK
DEN OEVER

Fig. 2 Chart of the western Wadden Sea (Netherlands). Deep gullies, functioning as migration routes, are indicated

With the cooperation of the three authors, of whom two are working in the northeast of Brazil, it was possible to try the SA-L method on Penaeus brasiliensis, a western Atlantic species (Fig. 1).

Periodically, mature specimens of P. brasiliensis attempt to migrate out to sea from the Alazão, an artificial marine lake of about 400 ha, which is used as a sea water reservoir for salt production near Macau, Rio Grande do Norte, Brazil (Fig. 3). The pattern of migration shows a clear lunar periodicity. On samples of migrating male and female shrimp, collected between 17 November 1975 and 30 September 1976, the SA-L method has been applied to check the possibility of growth between moults and patterned migration in this penaeid species.

Note: Since the vernacular name "brown shrimp" is used for both species, only the scientific names are used in this paper.

2. METHODS AND MATERIALS

2.1 Sampling Methods

To study the seasonal migration of C. crangon, results were used of surveys along the entire coastal area of The Netherlands, carried out in all months of the year over a period of 15 years (Boddeke, 1975). On these surveys, samples were taken with shrimp beamtrawls, mesh size in the cod-end 20 mm stretched. The length distribution of the catch was noted, measured from the caudal edge of the uropods to the cranial edge of the scaphocerites, and the density (numbers caught per 1 000 m^2) was determined. Sex was determined by external characteristics and verified by an extensive study of the gonad structure (Boddeke, 1966). Shrimps migrating pelagically toward inshore waters in early spring were caught from an anchored ship with a large plankton net fishing in midwater in the tidal currents (Postuma, 1969).

For the study of the migration of P. brasiliensis, results were used from commercial fishing with cast nets near the pump house of the Alazão lake during nights when the pumps were working. The number of fishermen involved was practically constant during the period of investigation. Fishing time was, normally, from 18.00 (sunset) to 22.00 h. During nights with very large catches the fishing continued for another one or two hours. During nights when, at most, very small catches could be expected after midnight, no fishing took place. For this study, samples of shrimp were taken from the commercial catch on several days.

Body length, measured from the caudal end of the telson to the point of the rostrum, was defined and the sex determined following the method of Perez Farfante (1969).

2.2 Method to measure Time Phase within the Intermoult Period (SA-L method)

C. crangon is able to grow within the intermoult period (Meixner, 1969). The cuticle of this shrimp is an elastic membrane in which the hard shields are embedded. By growth during the intermoult period body-length increases, but the surface area of the hard parts of the carapace does not change. This results in a regular shift in the relation between body-length and surface area of certain hard parts of the cuticle within the intermoult period.

To establish this relationship body-length was measured, as was the area of the dorso-lateral shields of the first three somites (tail segments), of samples of cooked shrimps, these samples being divided into berried females with unripe eggs, berried females with practically ripe eggs and non-berried females, and having been taken on several dates during the autumn-winter period of migration, over a period of several years. The technical details have been described extensively in an earlier paper (Boddeke, 1976). In P. brasiliensis fresh shrimp were used and only the dorso-lateral shield of the second abdominal somite was measured.

By plotting the surface area of one or more dorso-lateral shields (SA) against the square of body length (L^2) of a shrimp sample, a regression line of the form $y = b_o + b_1 x$ can be obtained in which y stands for the surface area (SA) and x for L^2. The parameters b_o and b_1 are not constant but have a particular value for each regression line representing a sample.

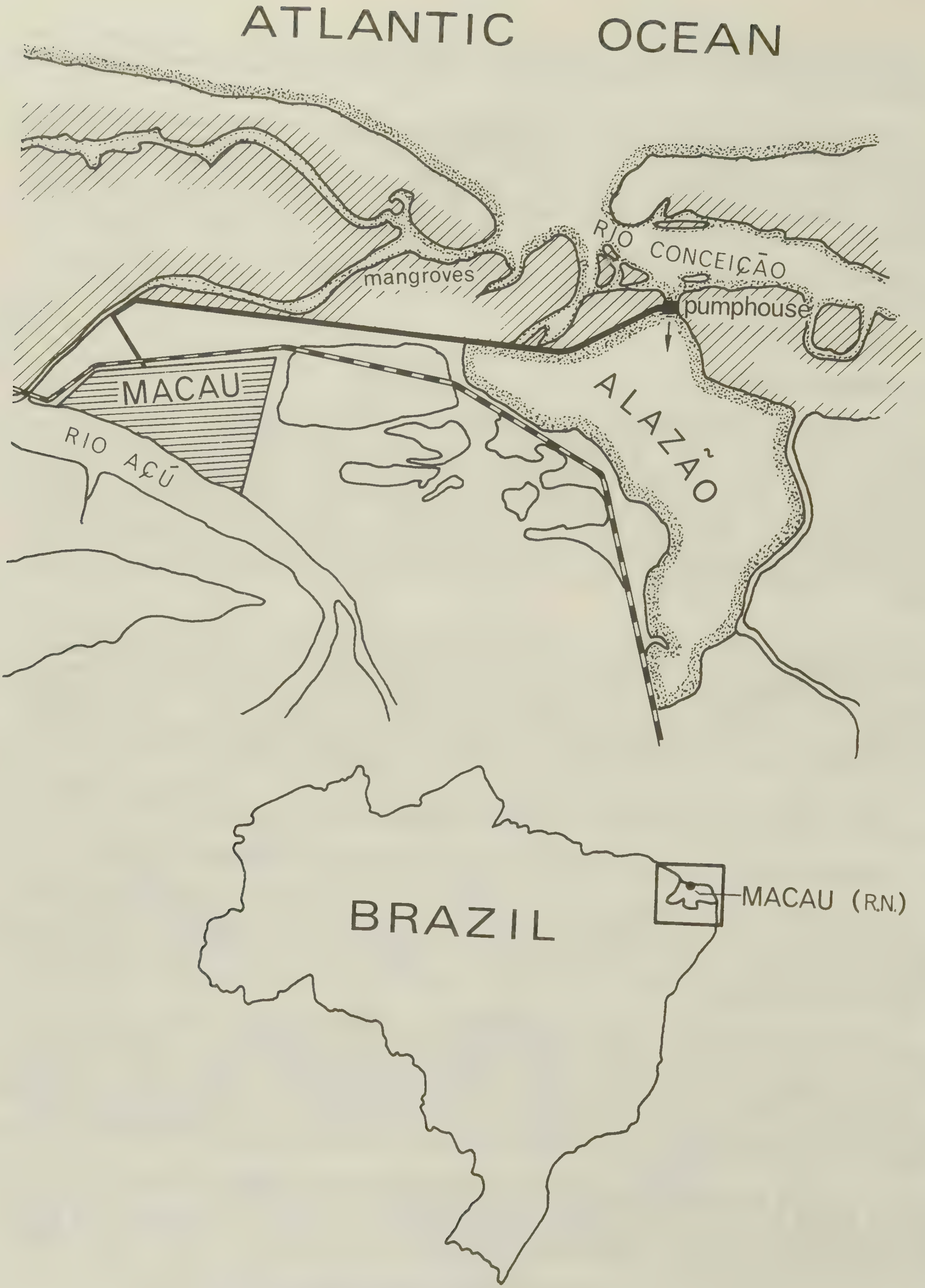
ATLANTIC OCEAN
mangroves
RIO CONCEIÇÃO
pumphouse
MACAU
RIO AÇU
ALAZÃO
BRAZIL
MACAU (R.N.)

Fig. 3 Chart of the Macau area (Rio Grande do Norte, Brazil) with the Alazão and the location of the pumphouse

For C. crangon, on several occasions in this article the position of the regression line is expressed by the calculated value of SA for a shrimp of 6.0 cm body-length in which the function, $SA = b_0 + b_1 \cdot L^2 = b_0 + b_1 \cdot 36$. That value is called SA-6.

In Fig. 4 the growth between two consecutive moults is shown for berried females of C. crangon caught on the IJmuiden beach during August and September 1970, well before the autumn-winter migration which starts in October. The high correlations (r = 0.96 and 0.97 respectively) in these two samples, reflect not only the strictly patterned distribution of C. crangon outside the nursery grounds but also the accuracy of the measuring technique.

For P. brasiliensis, samples of migrating females and males were taken on several dates within one lunar cycle. Due to the greater size of these penaeids, the calculated SA value for a shrimp of 10 cm was used on several occasions to express the position of the regression lines. This value is called SA-10.

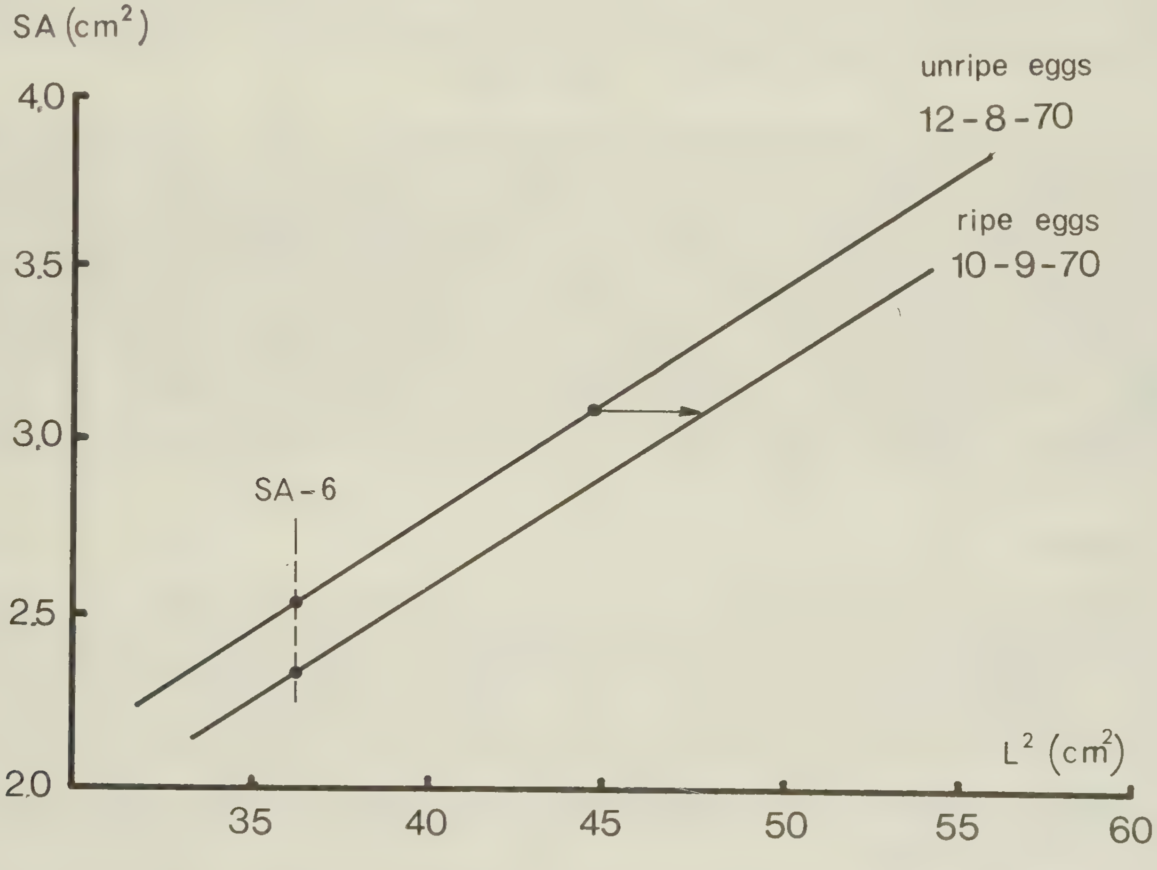

Fig. 4 Correlation between the surface area of the dorso-lateral shields of the first three tail segments (SA) and the square of body length (L^2) of berried females of Crangon crangon with unripe (light-coloured) eggs caught on 12 August 1970 (regression: $SA = 0.129 + 0.066\ L^2$, $r = 0.96$) and berried females with ripe (dark-coloured) eggs caught on 10 September 1970 (regression: $SA = 0.004 + 0.064\ L^2$, $r = 0.97$). The moving to the right of the regression line expresses the growth between two consecutive moults. Both samples caught on the IJmuiden beach

3. SEASONAL MIGRATION OF CRANGON CRANGON

3.1 General Description

Crangon is a dominant crustacean species along The Netherlands coast, due to its habitat requirements and the available environment. It is a typical inhabitant of soft, sandy or silty bottoms. Along the western European coast, commercially important populations of *C. crangon* are found only in areas where inshore waters such as inlets, estuaries and bays occur, which function as nursery grounds for juvenile shrimps. Shrimp larvae move inshore to these nursery grounds using tidal currents. Inshore transport of shrimp larvae is probably mainly passive and corresponds closely with the transport of silt particles in this area (Power, 1974).

Larvae of *C. crangon* are hatched throughout the year, but the period September-December is the least productive. The great numbers of larvae released in spring grow and develop in shallow coastal areas during summer, enlarging the biomass of the shrimp stock on the nursery grounds considerably. Shrimps hatched in May attain a length of 52 mm by September of the same year (Boddeke and Becker, 1976). The mechanism triggering migration in this species is, most probably, an accumulation of stimuli resulting from temperature fluctuations. In shallow inshore waters the influence of the air temperature on water temperature is considerable, particularly on tidal flats during high water. Along the North Sea coast differences between air and water temperature can be as much as 10°C during warm windless days in spring (April-May) and cold nights in autumn (October-November).

The first part of the autumn-winter migration, starting usually in October and taking place every year in a practically uniform way before 1 December, is the most important. This migration takes the sexually mature shrimps outside areas dominated by tidal flats (Havinga, 1930, v.d. Baan, 1975). The migration after 1 December depends greatly on the course of the winter and is highly variable in time, duration and distance. In an extremely mild winter virtually no further migration occurs. However, in a moderate to severe winter, sexually mature shrimps migrate from 1 to 50 mi offshore (Boddeke, 1975). The spring migration in the direction of the coast is not the opposite of the autumn migration but is a selective addition to the latter, by means of which an efficient distribution of the stock is further promoted. Only fertile males and large, sexually mature females take part in the spring migration. The females migrate mainly to the North Sea beach zone whilst the males migrate partially also to inshore waters. Spent males remain in deep water, changing to female sex in the period March-May (Boddeke, 1966 and 1976).

3.2 Pattern

A remarkable aspect of the autumn migration of *C. crangon* is the equal size composition of groups of migrating shrimps during the migration period. Migrating fertile males are small, mainly 35-45 mm. Migrating berried and non-berried females show an almost constant length distribution between 48 and 72 mm during the whole migration period. But in a moderate winter, non-berried females within this length group can be caught also in relatively large numbers in tidal gullies far inshore, after the autumn-winter migration has come to an end.

From these observations it became clear that the tendency to migrate is not related in the first instance to size or sexual category but to differences in the physiological condition of individual shrimps.

With the described "SA-L method", samples of berried and non-berried females caught on a migration route (Marsdiep area, Fig. 2) were investigated during a normal winter (1973-1974) and during a winter (1975-1976) that was extremely mild until February.

The shrimp stock on the Tesselstroom rose quickly in October 1974 as the result of migration from inshore areas, and decreased irregularly during the period November-January (Fig. 5). The most likely explanation for this decrease is that, during this period, the migration to the open sea from the Tesselstroom area was quantitatively of more importance than was continued migration to this area from the inner Wadden Sea.

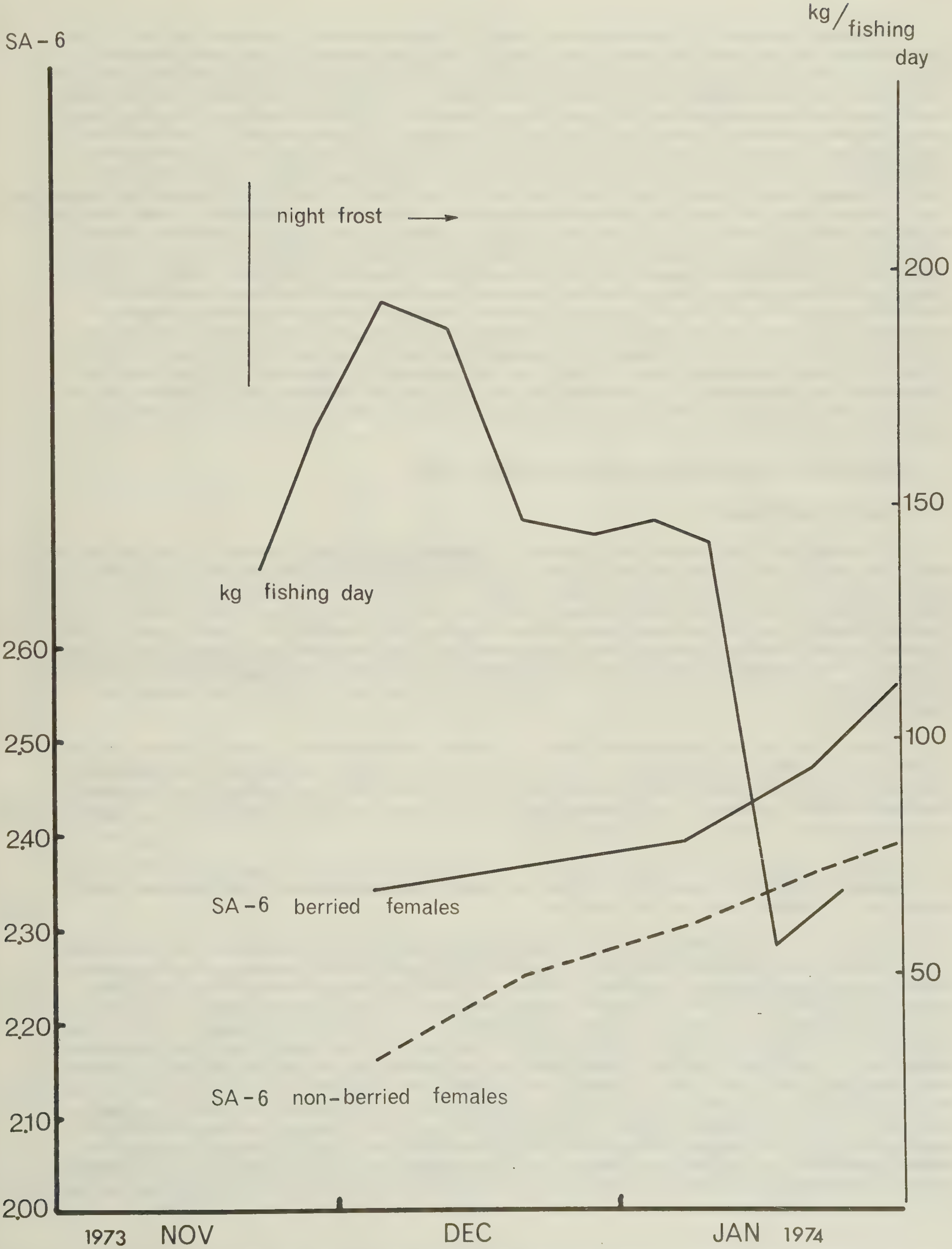

Fig. 5 Levels of SA-6 of migrating non-berried and berried females caught benthically in the Texelstroom area in the period December 1973-March 1974, in combination with the catch per fishing day in the same period. Species: Crangon crangon

The strict pattern of this migration could be demonstrated by the SA-L method. For both non-berried and berried females with unripe eggs the value for SA-L rose regularly during December and January (Fig. 5). This rise can be explained only by assuming regular replacement of the shrimps in the Tesselstroom area by shrimps farther away from the next moult than their predecessors, for this rise is opposite to the decrease of the SA-L by growth between moults. Taking into account the course of the migration, a rising value for SA-L implies a decreasing sensitivity to migration-triggering stimuli and a lesser sexual development, since berried shrimps cannot moult before the eggs hatch. For non-berried females longer than 46 mm, a moult at this time of the year is generally coupled with spawning. Fig. 5 shows that the SA-6 for migrating non-berried females is considerably lower than for migrating berried females. This suggests that, on average, non-berried females are less sensitive to migration-triggering stimuli than berried females. This is in line with the wintering of considerable numbers of large non-berried females in shallow inshore waters during a moderate winter, while berried females then disappear from there completely. In the winter of 1975-1976, when the air temperature was mild during the period November-December 1975, and even no night frost occurred before January, the values for SA-L for both berried and non-berried females decreased considerably during November and December (Fig. 6). This decreasing value for SA-L can be explained by assuming that the regular replacement by migration of the shrimps in this area by new migrants with a higher value for SA-L was so insignificant during this period, that it was dominated by the effect of growth between moults.

4. MIGRATION OF PENAEUS BRASILIENSIS FROM THE ALAZÃO

4.1 General Description

In the period October-May individuals of Penaeus brasiliensis attempt to migrate to sea from the Alazão lake. They gather in the vicinity of the pump house during nights when the pumps are working. Through these pumps, water is brought into the lake at a rate of 300 m^3/min, causing an inshore directed current which can be compared with a flood stream. In the Alazão, however, an "ebb stream" never occurs under normal conditions. Under natural conditions the ebb stream is used by adult penaeids for their seaward migration. This is demonstrated for example by the fishing for migrating specimens of Penaeus vannamei on the lagoons along the Pacific coast of Mexico with "tapos", traps barring a creek, functioning only during ebb.

However, it is not unreasonable that, in natural circumstances, adult penaeids ready to migrate are stimulated to pelagic behaviour by the flood tide. By appearing pelagically at the end of the flood tide, they utilize fully the first hours of the ebb tide, when the current velocity is high. Such a mechanism is described for adult specimens of C. crangon migrating inshore in spring (Boddeke, 1976).

In the Alazão tidal differences cannot be the cause of the fluctuations of the catch corresponding with the lunar cycle, since the pumps work practically independent of the height of the water level on the seaside.

It is more likely that moonlight plays an important role in regulating the migration, which accords with the observations of Wheeler (1937), who found in several shrimp species, including P. brasiliensis, a rhythmic pattern of activity and quiescence over the lunar periods. Wheeler came to the conclusion that the most likely cause of periodic swarming is the direct inhibitory effect of light. If moonlight is an inhibiting factor in the migration to sea of adult shrimps, in this migratory process, it is likely that the physiological condition of individual shrimps, being more or less sensitive to the inhibitory influence of the moonlight, must play a role, taking into account the appearance of shrimps near the pump house even during full moon. Although P. brasiliensis do not change sex like C. crangon, moulting is also a central process in the life cycle of this penaeid, being coupled with growth and, for the female, with copulation (Perez Farfante, 1969). For this reason it seemed justified to use the SA-L method for this species also as a measure for the physiological condition.

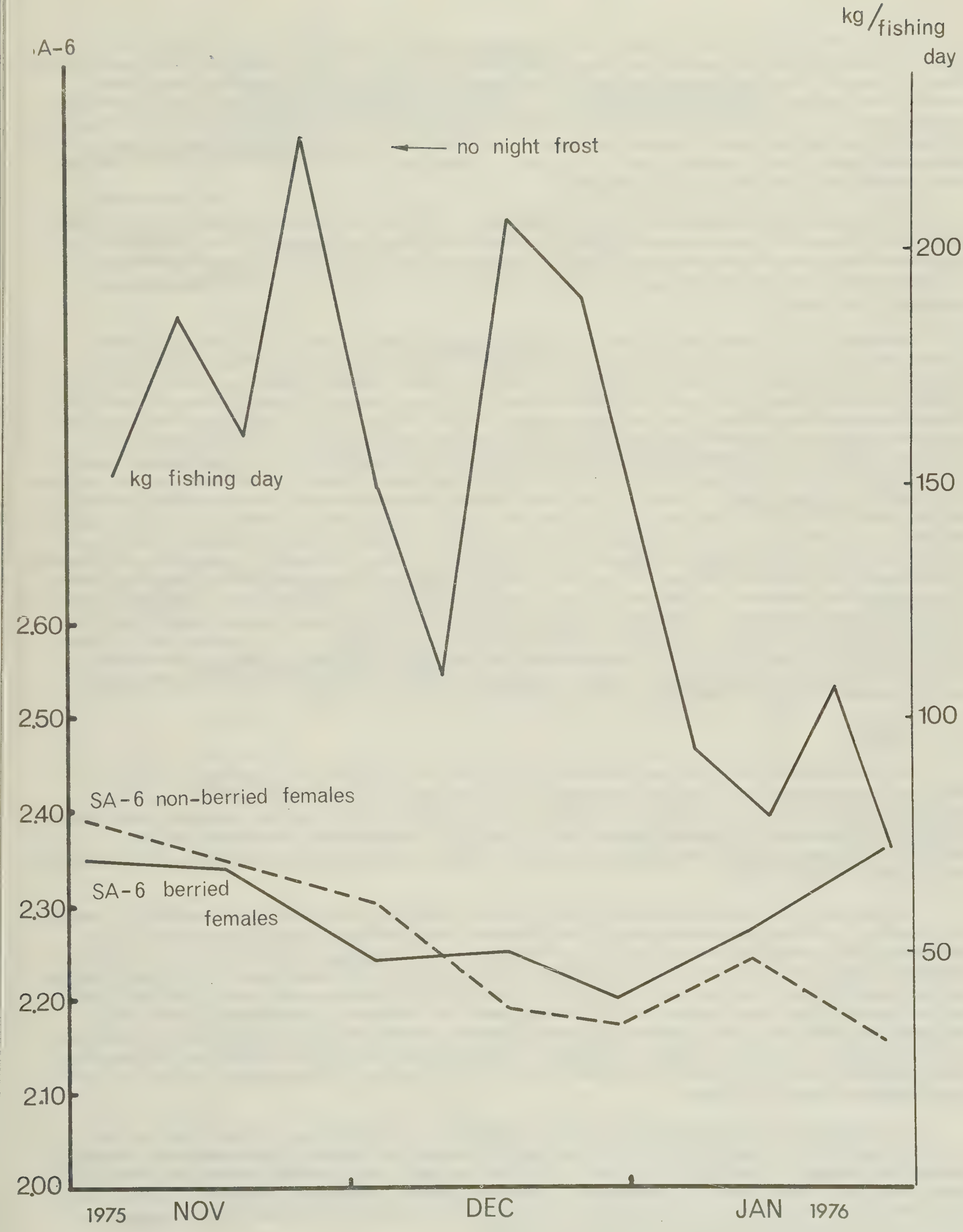

Fig. 6 Levels of SA-6 of berried and non-berried females during a winter period without mass migration, in combination with the catch per fishing day. Texelstroom area 1975-1976. Species: Crangon crangon

During the lunar month, samples of males and females were taken from catches near the pump house on different dates, including both the dark night with no moon and the night before the full moon. The length composition of the samples was the same throughout the lunar month. The shrimp were 80-120 mm long, the females on average 5-6 mm longer than the slower growing males. To these samples the SA-L method was applied. With the exception of Sample I, collected during the night before full moon, the correlation (r) between SA and L^2 was extremely high in all samples, and in the case of Samples II, III, IV, V and VII of females, even exceptional for biological research.

The differences between the SA-10 of samples of males and females collected on the same date (the values for the males being mostly lower than for the females) are of interest in respect of the suggestion of Racek (1959) concerning the existence of a lunar periodicity in the ecdysis for adolescent and adult specimens of the Australian species *Metapenaeus macleayi* (see also 5.2).

However, it is clear that males of *P. brasiliensis* grow slower than females as was proved by our observations on the growth of these shrimp in ponds. For this reason, the relation between SA and L^2 will shift more slowly in males than in females, resulting in a higher value for SA-10 for males than for females in the intermoult phase if both moult at the same moment and start from the same maximal value for SA-L. The difference between the highest and lowest observed values of SA-10 of samples being almost equal for males and females (Table III) demonstrates that, in both sexes, the possibility to grow between moults is utilized fully. The combination of these facts excludes a lunar periodicity in the ecdysis for adult *P. brasiliensis*. This is confirmed further by observations on specimens kept in a pond from the post-larval stage. The observed regular difference between the SA-10 values of males and females can be explained satisfactorily by assuming the existence of patterned migration in *P. brasiliensis* analogous to *C. crangon*, in which species a comparable difference was observed in the SA-6 values of migrating non-berried and berried females (Fig. 5). For *C. crangon* the explanation was sought in a lower sensitivity for migration-triggering stimuli of non-berried females. In the case of *P. brasiliensis* males should be more sensitive than females to the inhibiting influence of the moonlight on migration. This assumption is supported by data of de Bondy (1968), who found, for migrants of *Penaeus duorarum* in Senegal, a difference in the percentage of males in catches regulated according to the lunar month, being somewhat higher around the first quarter than around the last.

4.2 Pattern

In the catches near the pump house a sharp peak occurs around the new moon (Fig. 7). Much smaller catches are taken between full moon and the last quarter. Around the first quarter practically no fishing takes place, as only small catches can be expected after midnight, for which the fishermen cannot wait. In Fig. 7 the catches during the period October 1975-January 1976 are combined with the values for SA-10 of the samples, both arranged to follow the lunar month.

The period of large catches from last to first quarter is coupled with decreasing values for SA-10. At other dates much smaller catches are coupled with higher values for SA-10. Following the conclusion derived from the research on *C. crangon*, and taking into account the observations of Wheeler about the influence of moonlight on the behaviour of *P. brasiliensis*, we can presume that the decreasing value for SA-10 of the shrimp caught near the pump house in the period from last quarter to full moon, means an increasing sensitivity to stimili triggering migration. This results in large catches around new moon, exhausting quickly the available stock of shrimp ready to migrate. After the new moon, the inhibiting influence of the moonlight becomes gradually stronger practically blocking the migration during the two-week period around full moon.

The moonlight as an inhibiting factor is subject to interfering factors such as water-clarity and clouds (Wheeler, 1937). Since only the real influence of the moonlight counts, a regular course of the values for SA-L of migrating males and females during the lunar month can occur only under ideal circumstances. However, these interfering factors do not affect the patterned character of the migration, which is even more strict than in *C. crangon* in view of the correlation given in Tables I and III.

TABLE I

Correlation between SA and L^2 of consecutive samples from the Tesselstroom area in a normal winter

Migrating non-berried females

Sample	Date	Number of individuals	Regression	SA-6	r
I	04.12.73	40	$SA = 0.1975 + 0.0544 \cdot L^2$	2.16	0.866
II	20.12.73	40	$SA = 0.1948 + 0.0572 \cdot L^2$	2.25	0.969
III	07.01.74	40	$SA = -0.0215 + 0.0645 \cdot L^2$	2.30	0.929
IV	21.01.74	40	$SA = -0.0773 + 0.0678 \cdot L^2$	2.36	0.958
V	01.02.74	40	$SA = 0.0671 + 0.0645 \cdot L^2$	2.39	0.920

Migrating berried females with unripe eggs

Sample	Date	Number of individuals	Regression	SA-6	r
I	04.12.73	40	$SA = -0.0614 + 0.0668 \cdot L^2$	2.34	0.876
III	07.01.74	40	$SA = -0.2332 + 0.0730 \cdot L^2$	2.39	0.948
IV	21.01.74	40	$SA = -0.0055 + 0.0688 \cdot L^2$	2.47	0.975
V	01.02.74	40	$SA = 0.0234 + 0.0704 \cdot L^2$	2.56	0.959

TABLE II

Correlation between SA and L^2 of consecutive samples from the Texelstroom area in a very mild winter

Non-berried females

Sample	Date	Number of individuals	Regression	SA-6	r
I	03.11.75	47	$y = 0.1314 + 0.0196 \cdot L^2$	2.39	0.891
II	17.11.75	48	$y = 0.0297 + 0.0220 \cdot L^2$	2.35	0.932
III	03.12.75	48	$y = -0.0594 + 0.0240 \cdot L^2$	2.30	0.958
IV	17.12.75	48	$y = -0.0910 + 0.0238 \cdot L^2$	2.19	0.976
V	30.12.75	48	$y = -0.0599 + 0.0227 \cdot L^2$	2.17	0.978
VI	13.01.76	48	$y = -0.0950 + 0.0244 \cdot L^2$	2.24	0.962
VII	27.01.76	40	$y = 0.0621 + 0.0192 \cdot L^2$	2.15	0.927

Berried females with unripe eggs

Sample	Date	Number of individuals	Regression	SA-6	r
I	03.11.75	48	$y = -0.1375 + 0.0273 \cdot L^2$	2.35	0.946
II	17.11.75	48	$y = 0.0244 + 0.0227 \cdot L^2$	2.34	0.929
III	03.12.75	48	$y = 0.0545 + 0.0209 \cdot L^2$	2.24	0.912
IV	17.12.75	48	$y = -0.0638 + 0.0243 \cdot L^2$	2.25	0.970
V	30.12.75	48	$y = -0.0036 + 0.0221 \cdot L^2$	2.20	0.941
VI	13.01.76	48	$y = -0.1167 + 0.0260 \cdot L^2$	2.27	0.971
VII	27.01.76	40	$y = -0.0879 + 0.02604 \cdot L^2$	2.36	0.945

TABLE III

Correlation between SA and L^2 of samples of *Penaeus brasiliensis* migrating from the Alazão (Rio Grande do Norte, Brazil), caught near the pump house

Males

Sample	Date	Number of individuals	Regression	SA-10	r	Mean body length mm
I	17.11.75	25	$SA = 0.8137 + 0.0196 \cdot L^2$	2.77	0.697	95.8
II	24.11.75	25	$SA = 0.0435 + 0.0290 \cdot L^2$	2.94	0.978	91.0
III	01.12.75	26	$SA = 0.3301 + 0.0245 \cdot L^2$	2.78	0.946	92.3
IV	03.12.75	24	$SA = 0.2222 + 0.0259 \cdot L^2$	2.81	0.945	91.4
VI	13.05.76	23	$SA = 0.311 + 0.0269 \cdot L^2$	3.00	0.970	109.7
VII	20.05.76	23	$SA = 0.132 + 0.0288 \cdot L^2$	3.01	0.968	110.4
VIII	30.09.76	30	$SA = -0.354 + 0.0320 \cdot L^2$	2.845	0.968	98.0
Caught on a distance of 1 km from the pump house:						
V	03.12.75	17	$SA = -0.0286 + 0.0293 \cdot L^2$	2.901	0.964	85.2

Females

Sample	Date	Number of individuals	Regression	SA-10	r	Mean body length mm
I	17.11.75	35	$SA = 0.0867 + 0.0272 \cdot L^2$	2.81	0.919	99.4
II	24.11.75	30	$SA = -0.2715 + 0.0325 \cdot L^2$	2.98	0.994	102.8
III	01.12.75	34	$SA = -0.1878 + 0.0307 \cdot L^2$	2.88	0.982	96.4
IV	03.12.75	26	$SA = -0.0632 + 0.0293 \cdot L^2$	2.87	0.980	95.6
VI	13.05.76	24	$SA = 0.3497 + 0.0264 \cdot L^2$	2.99	0.930	117.3
VII	20.05.76	20	$SA = 0.209 + 0.028 \cdot L^2$	3.04	0.989	117.0
VIII	30.09.76	29	$SA = -0.405 + 0.0320 \cdot L^2$	2.795	0.943	104.8
Caught on a distance of 1 km from the pump house:						
V	03.12.75	24	$SA = -0.1169 + 0.0305 \cdot L^2$	2.933	0.983	83.3

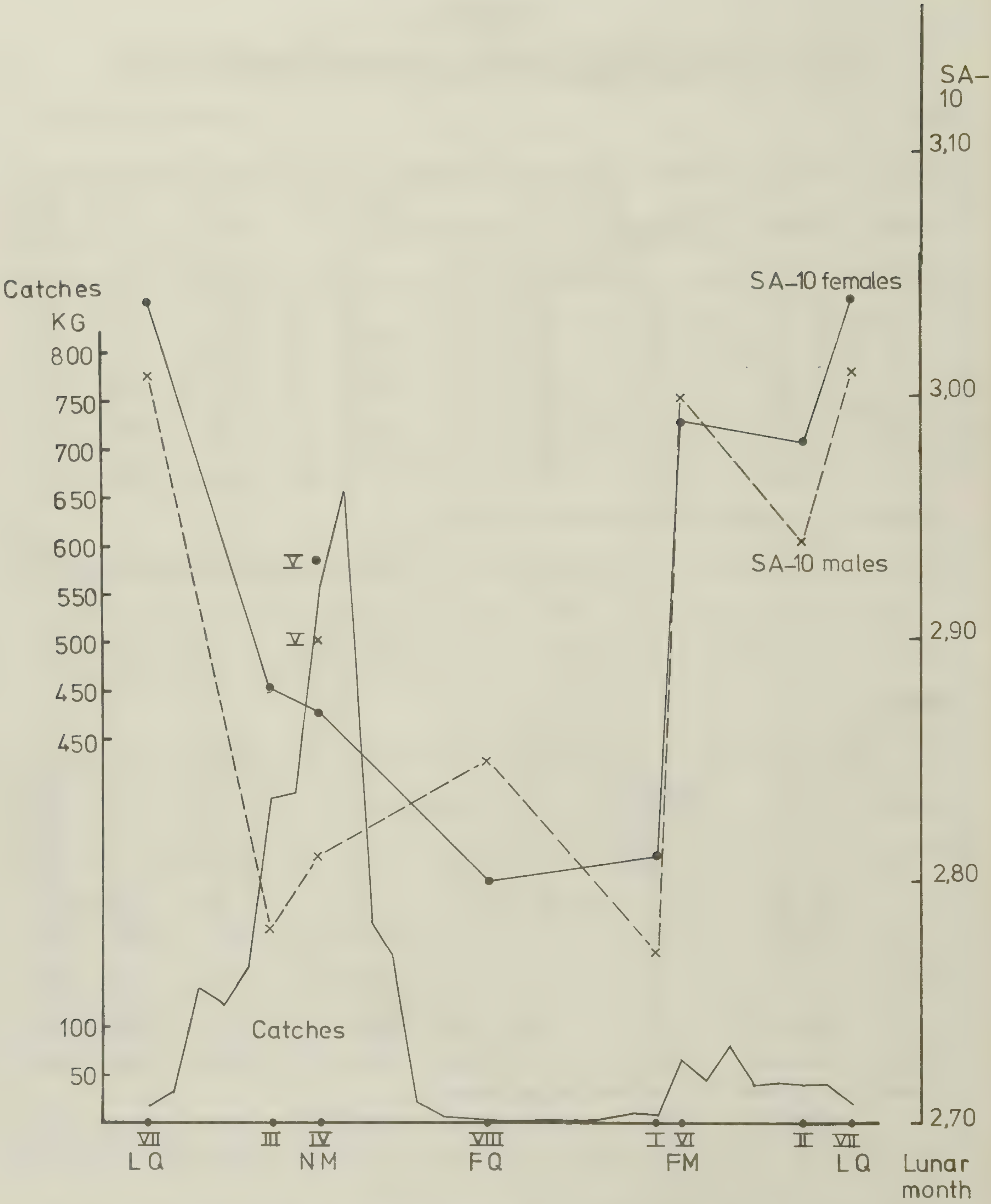

Fig. 7 Summed catches of Penaeus brasiliensis in the Alazão near the pumphouse in the period October 1975-January 1976, arranged by lunar month, in combination with the levels of SA-10 of males and females

5. DISCUSSION

5.1 Comparison of the Life Cycles of Crangon crangon and Penaeus brasiliensis

The life cycles of these two shrimp species show many similarities despite taxonomic and geographical differences. Both species inhabit coastal areas and prefer soft silty (juveniles) or sandy (adults) bottoms. The larvae move to shallow nursery grounds, where they grow up. Growth is rapid in both species. According to our observations, females of both species can, under favourable conditions, reach the minimum size of sexually mature shrimps (5 cm for C. crangon and 14 cm for P. brasiliensis) in four months (Paiva Ferreira de Souza, 1974; Boddeke and Becker, 1976).

The production of larvae of both species takes place almost throughout the year. In C. crangon larvae are scarce during the period September–January (Boddeke and Becker, 1976), and P. brasiliensis larvae are scarce between November and March (Novoa, Campos and Rojas, 1976). In both species the migration to the open sea of sexually mature specimens is not essential for reproduction. C. crangon, landlocked in artificial marine lakes in the south of The Netherlands (Veerse Meer, Grevelingen), proved capable of reproducing there (Boddeke, 1963). According to our observations, P. brasiliensis reproduces in the Alazão. This conclusion is based on the presence of females with ripe ovaries and the appearance of numerous juveniles after the pumps have been inactive for four months. In both species the migration to the open sea cannot be considered an escape from unfavourable environmental conditions since C. crangon, at all stages of its life cycle, can stand even the most extreme seasonal variations (Boddeke, 1963, 1976). The stable climatological conditions in tropical waters make such an escape highly unlikely in the case of P. brasiliensis, particularly in the case of this lake with its very stable salinity of about 40 ‰. Adult specimens of P. brasiliensis can withstand salinities up to 60 ‰, as was proved by our experiments in ponds.

5.2 Biological Significance of patterned Migration and Distribution

Both C. crangon and P. brasiliensis have a dispersed spawning during a large part of the year and occur often in low densities. The densities in which adult shrimps occur in general are often overestimated. Opinions on densities of adult shrimps are often based on juvenile shrimp densities in shallow inshore waters or apparent large numbers caught by trawling.

If we consider the catch per fished area of commercial trawlers as a measure of adult shrimp density, although commercial shrimpers fish by preference on places with high concentrations of shrimp, densities of adult shrimps are rarely impressive. In the Dutch fishery for brown shrimp a very good catch is made if one shrimp longer than 54 mm is caught per 2 m^2 fished. However, in periods when shrimps are scarce, densities of 1 shrimp (caught) per 20 m^2 are fished commercially. In Penaeus fishing the density figures are still lower. In the Tortugas fishing for Penaeus duorarum, an average catch is made when 1 shrimp of commercial size is caught per 166 m^2 fished and commercial fishing is still possible when 1 shrimp is caught per 300 m^2. These figures hold generally for the Gulf of Mexico and the Guyanas (Dr. Albert Jones, Miami, personal communication).

Taking these low densities into account, the existence of rigid patterns of distribution and migration maintaining shrimps in the same physiological condition as a group is a biological necessity to ensure a maximum reproduction potential. For this reason the described migration pattern probably exists in other shrimp species.

The described migration pattern from estuarine waters to open sea can explain very well the observations of Racek (1959) on the school prawn (Metapenaeus macleayi) occurring in eastern Australian waters. The biological characteristics of the species, as described by Ruello (1976), are very similar to those of Penaeus schmitti and, to a rather lesser extent, to those of P. brasiliensis, both from the Caribbean region. Racek found a lunar periodicity in the percentage of soft-shelled school prawns caught commercially in estuarine waters in New South Wales. There was a sudden increase in the percentage of soft-shelled prawns beginning on the tenth day after the new moon with peak values ranging from the 13th to 16th day. The following decline was, nearly always, comparatively slow towards the 21st day, with a pronounced fall during the two days following the new moon. In this species also a lunar periodicity in catches in estuarine waters could be demonstrated. Commercial catches were restricted to the period from three days before the last quarter to four days after the new moon, which is similar to the fluctuations in the catch of P. brasiliensis in the Alazão, as shown in Fig. 7.

It is also very interesting to compare the migration of P. brasiliensis with the spawning migration to the open sea of the European eel (Anguilla anguilla), which migrants are called silver eels (Deelder, 1970). Lowe (1952) found that silver eels congregate near the outflow of a lake and there await a stimulus (e.g., a "flood") to migrate further. Catches of silver eels on migration routes, arranged in order of the lunar month, show a clear lunar periodicity with the highest catches around last quarter (Jens, 1952-1953 and Deelder, 1954).

6. SUMMARY

In three previous papers on the biology of the western European shrimp (Crangon crangon), a method has been described to demonstrate the rigid patterns in migration and distribution of this species. The sensitivity to migration-triggering stimuli of C. crangon depends on the sexual category (berried females are more sensitive than non-berried females) and also on the physiological condition of the individual shrimp within these categories. The physiological condition is measured indirectly by defining the phase of the moulting cycle. Shrimp (Crangonidae and Penaeidae) increase in length between two consecutive moults by stretching the elastic parts of their cuticles. Since the body length increases while the hard parts of the cuticle do not, the relation between the surface area of certain shields of the cuticle (SA) and the body length shifts during the intermoult. This shift offers a means of determining the intermoult phase of the shrimp. It was found that the sensitivity to migration-triggering stimuli decreases the further the shrimp is away from the next moult. Among different waves of migrating shrimp a high measure of synchronization could be demonstrated in respect of the moulting cycle.

The same method has been applied to specimens of Penaeus brasiliensis attempting to migrate from a salt water pond in the northeast of Brazil. The results obtained show a striking similarity to the migration pattern of Crangon crangon in the North Sea, suggesting strongly the existence of comparable rigid migration and distribution patterns in this penaeid

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THE OSCILLATORIA ERYTHRAEA (CYANOPHYTA) COMMUNITY OF ASSOCIATES

by

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1. INTRODUCTION
2. DISCUSSION
3. CONCLUSIONS
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Abstract

The colonial, filamentous blue-green alga Oscillatoria erythraea Drouet (= Trichodesmium) is found to serve as a pelagic minisubstrate in which, sometimes, complex micro-communities develop. As the algae age, a polysaccharide mucilage accumulates which acts as an apparently very favourable matrix for several associated organisms.

Bacteria, fungi, free-living protozoans (including encysted Peridinium trochoideum) and pennate diatoms all may be present in large numbers. A new family of Hydroidea, Pelagiana trichodesmiae is also found attached.

A preliminary description of these associations and their possible significance in the open ocean is given.

Resumen

Se ha hallado que el alga verde-azul filamentosa Oscillatoria erythraea Drouet (= Trichodesmium), que vive en colonias, actúa como minisubstrato pelágico en el que a veces se desarrollan microcomunidades muy complejas. A medida que las algas envejecen se acumula un mucílago polisacaroide que actúa como matriz, aparentemente muy favorable, para varios organismos asociados.

Se pueden hallar en gran número bacterias, hongos, protozoos libres (incluso Peridinium trochoideum enquistados) y diatomeas peniformes. Se ha encontrado también una nueva familia de Hydroidea, Pelagiana trichodesmiae.

En el trabajo se da una descripción preliminar de esas asociaciones y de su posible significado en alta mar.

1. INTRODUCTION

The genus *Oscillatoria* (= *Trichodesmium*) includes several filamentous colonial species of marine pelagic cyanophytes common in the tropical and subtropical regions of the oceans. In the western Atlantic and Caribbean regions, the *Oscillatoria* often contribute more than fifty percent of the surface chlorophyll or phytoplankton biomass (Margalef, 1965). In this paper, we give a preliminary description of the diverse community of organisms found living together in the blue-green colonies classified as *O. thiebautii* and *O. hildenbrandtii* by Sournia (1968) and lumped together with all other marine *Oscillatoria* into the species *O. erythraea* Drouet (1968).

In this paper we adopt Drouet's classification and differentiate only with respect to the two colony conformations exhibited by *O. erythraea*: a 'radial' arrangement of trichomes or filaments radiating from a common central area and a 'parallel' conformation of trichomes arranged more or less in parallel, in close contact with one another along most of their length. Both colony types show great variation in number of trichomes and cells. Radial colonies may average seventy-five cells per trichome and sixty trichomes per colony, while parallel colony trichomes are longer, perhaps two hundred cells per trichome with forty trichomes per colony.

O. erythraea trichomes do not secrete a thick polysaccharide sheath as do some of the Oscillatoriaceae. In radial colonies, however, a tenacious, mucilaginous material accumulates among the dense tangle of trichomes at the centre of the colony, forming a matrix which may harbour large numbers of a variety of organisms. Staining techniques show this matrix to be an heterogeneous carboxylated polysaccharide, perhaps comprising mainly glucose and mannose units. These two carbohydrates have been found by Japanese workers to be the most abundant in hot water fractions of *Oscillatoria* collected from the Kuroshio Current (Nobuhiko, 1975), and are common among the 'extra-cellular carbohydrates' produced by many blue-greens (Wolk, 1973).

2. DISCUSSION

The origin of this mucilage matrix is not clear. However, we have isolated from radial colonies bacteria which develop mucoid colonies on solid media, and have often observed pennate diatoms known to secrete mucilage in the benthos. Many unidentified unicellular organisms in the matrix seem to be embedded in their own mucilage. It is likely therefore that the composition of any one matrix is quite heterogeneous, depending upon the organisms within it. In addition, the mucilage must retain a large proportion of the organic products of bacterial and fungal degradation, and secreted metabolites from all the associated organisms. The retention by the mucilage of much of the *Oscillatoria* protoplasm and pigment after algal death and cell lysis results in a detritus particle which is distinctive and easily recognizable.

The structural strength provided by the matrix makes the radial conformation better able to withstand turbulence than the parallel form, and therefore a better basis for a community. Although both types of *Oscillatoria* colonies can harbour large numbers of micro-organisms,these communities differ considerably owing to the complete absence of the matrix in parallel colonies.

Bacteria are the most numerous members of the community, present in large numbers in over 85% of all colonies examined, and more abundant in the radial conformation. A huge diversity of bacterial morphologies and motilities has been recorded. Almost omnipresent is a tiny, highly motile rod, but most other forms occur sporadically and in variable numbers. The great variability of bacterial populations, even among several colonies of the same conformation from a single tow, suggests these populations result from accidental encounter and opportunistic growth. Though some bacteria doubtless act as a food source for other members of the community, their primary function must be mineralization.

The matrix of the radial colony appears to be a favourable substrate for at least two fungi, a filamentous form, probably a phycomycete (Dr. J. Kohlmeyer, Institute of Marine Sciences, University of North Carolina, Morhead City, North Carolina 28557, personal communication) previously mentioned by Margalef (1965), and a chytrid. Fungal zoosporangia are common in radial colony matrices, but are never seen in parallel colonies, or attacking intact algal filaments. Thus it appears that the mucilage is a prerequisite for the establishment of a fungal population which is primarily saprophytic.

A small assortment of bacteriophagous and saprophytic protozoans have been observed, with no obvious carnivores or attached forms. When free-living flagellates or ciliates are found they are often abundant, suggesting again accidental encounter followed by rapid growth in response to a favourable environment. Most hypotrichous and tetrahymenid protozoans are, probably, only temporary residents of the colony.

Cysts of the dinoflagellate *Peridinium trochoideum* are often present, embedded in the matrix of radial colonies. We have observed all stages of the life cycle of *P. trochoideum* in *Oscillatoria* colonies and this association may be of considerable importance to the dinoflagellate's success in pelagic areas (Borstad, in preparation). Less frequently found is another, larger dinoflagellate species, probably a *Gonyaulax*. Neither dinoflagellate is found associated with parallel colonies.

Both radial and parallel colonies often harbour large populations (three hundred or more individuals) of pennate diatoms, the most common species being *Nitzschia longissima*, *N. closterium*, *Synedra* spp., *Navicula* spp. and *Amphiprora* spp., with perhaps fifteen other species occurring in lesser numbers. As one might expect, there are differences in species present in parallel and radial colonies. Truly benthic species such as *Cocconeis scutellum*, *Acnanthes* and *Amphiprora* are found in large, actively dividing populations in the radial colony matrix, but never in parallel colonies. The diatoms most successful in parallel *Oscillatoria* colonies are those long needle-shaped species such as *N. closterium* and *N. longissima* and, to a lesser extent *Synedra* and *Navicula* species. The streamlined shape of these species and their motility permits them to penetrate the algal filaments, thus increasing their surface contact with the algae and, perhaps, nutrient exchange. Both *N. closterium* and *Synedra* do show a strong positive chemotaxis to lysing filaments, and a lesser positive reaction to the colonies themselves.

A previously undescribed hydroid has been regularly discovered embedded in the matrix of radial colonies, and has been assigned to the newly erected family Pelagianidae, in the order Anthomedusae (Borstad and Voss, in preparation). *Pelagiana trichodesmiae* is the minute athacate polypoid stage most often observed. The gonophores and medusae have been collected a few times only.

Pelagiana has not been found on other substrates at Barbados, and appears to be truly pelagic. It has been found in radial *Oscillatoria* colonies from widespread areas of the tropical Atlantic (personal communication, Dr. E. Carpenter, Marine Sciences Center, S.U.N.Y., New York).

Similar to other hydroids (Christensen, 1967), *Pelagiana* polyps are extremely voracious and consequently could constitute a significant component of the euphotic zone food webs. In ageing *Oscillatoria* populations, as many as 40% of the radial colonies may have 3-6 *Pelagiana* polyps.

The largest associate of both radial and parallel *Oscillatoria* colonies are the juvenile forms of the copepod *Macrosetella gracilis*, previously reported by Björnberg (1965). We have, however, never been able to discern whether or not they were actually eating the *Oscillatoria* cells. Although they do move about actively on the colonies, often agitating the trichomes violently, we have never observed cell lysis or disappearance of any algal trichomes. It is possible *M. gracilis* nauplii and copepodites are feeding on one or more of the associated organisms.

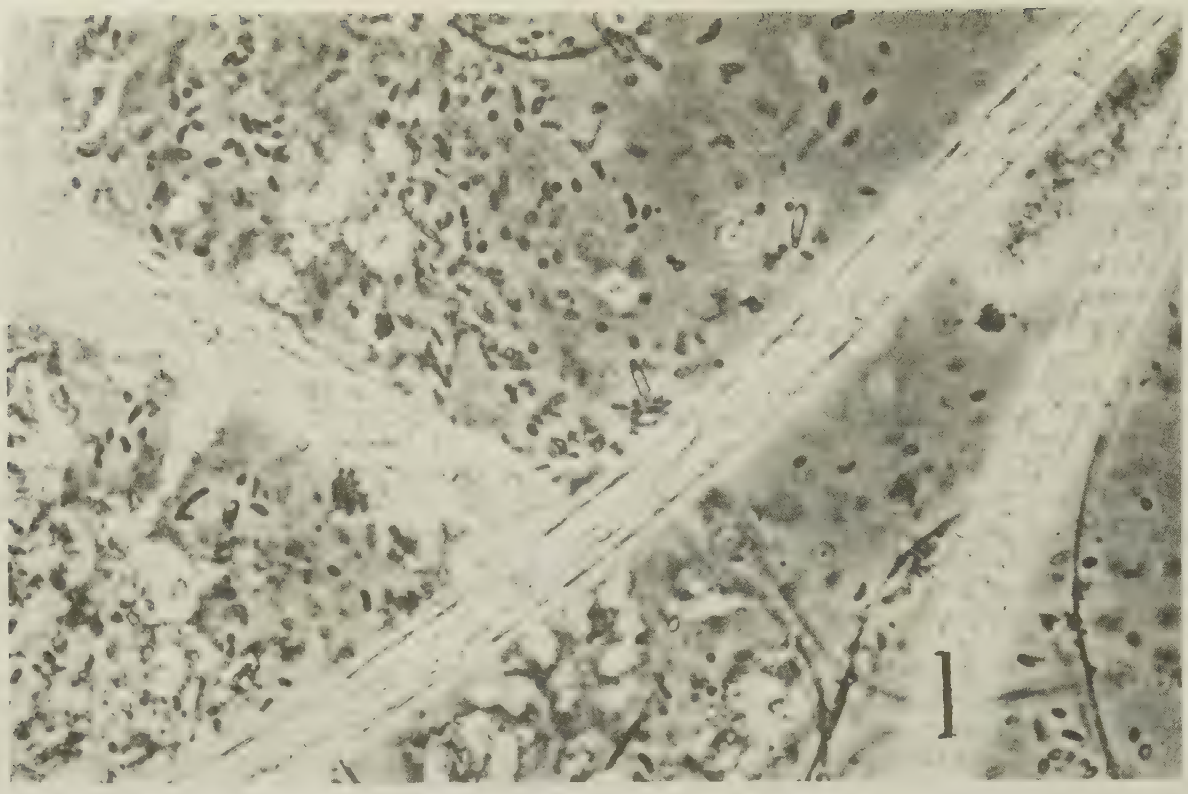

Fig. 1 Large varied bacteria population (scale line = 10 um)

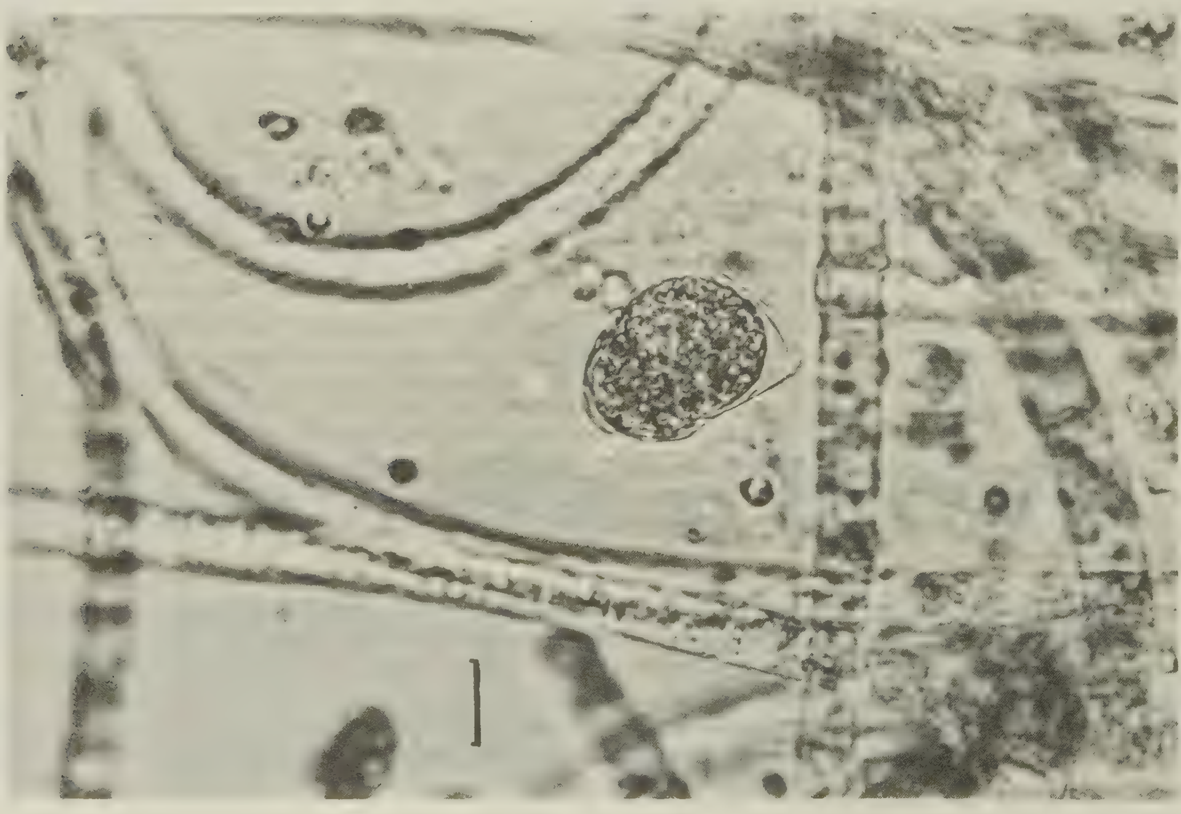

Fig. 2 Young Peridinium trochoideum cyst newly released from its theca

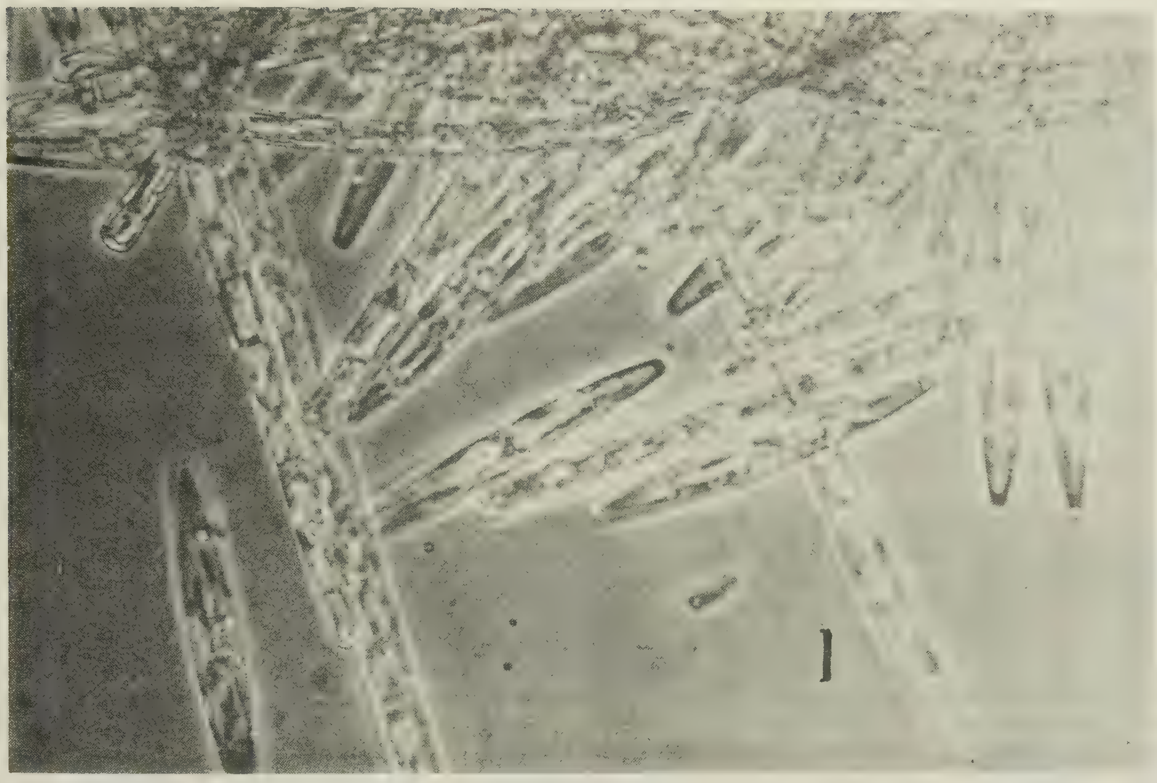

Fig. 3 Part of a large population of naviculoid pennate diatoms, clustered around radial Oscillatoria matrix (scale line = 10 um)

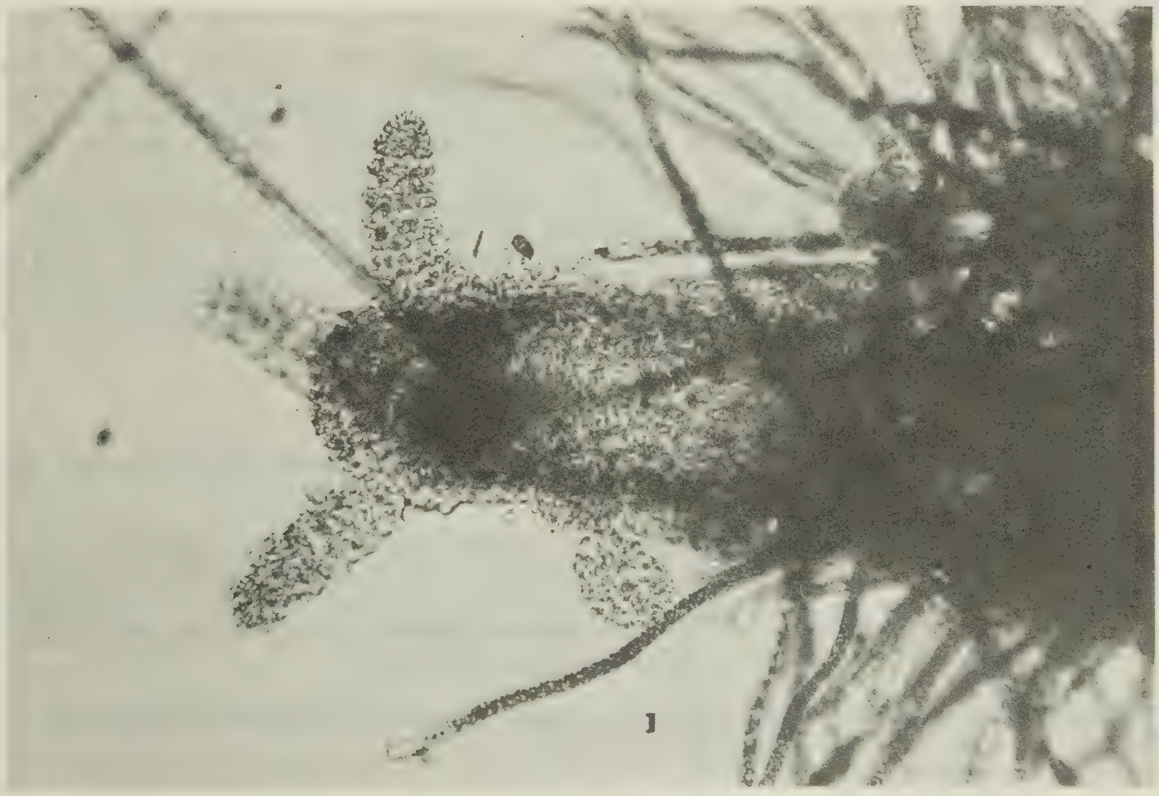

Fig. 4 Newly described athecate hydroid Pelagiana trichodesmiae, with partially contracted tentacles; note gonophores (scale line = 10 um)

There are several advantages to be gained by the organisms grouped in the community described here. Oscillatoria presents an abundant, widespread pelagic substrate available for colonization. The positive bouyancy provided by the algae's gas vacuoles ensures that attached organisms are retained in the euphotic zone, at least for the life of the algal colonies. In this respect Oscillatoria may be important for the long distance dispersal of one or more associates, particularly the encysted forms.

There is, probably, some nutrient exchange among members of the community in such intimate contact with one another. The mucilage in radial colonies probably retains excreted metabolites and regenerated nutrients of bacterial and fungal degradation, resulting in high localized concentrations of these compounds. Processes such as nitrogen fixation, or the activity of special enzymes such as alkaline phosphatase will, to some extent, benefit all members of the community.

3. CONCLUSIONS

For many of the associates, adhering to, and becoming part of, a larger particle such as Oscillatoria will afford them some protection from grazing predators. Where active Pelagiana hydranths are present this protection will be somewhat more complete.

The quantitative importance of the Oscillatoria community is difficult to assess from the data we have gathered thus far. The number of colonies with a well developed matrix observed at any one time seems to depend upon the age distribution of the Oscillatoria population sampled. At Barbados, we often see large populations of apparently actively growing Oscillatoria, few of which have well developed matrices. When smaller, more static populations are sampled, a larger proportion of the Oscillatoria colonies contain associated organisms. It should be stressed that interpretation of experimental data for photosynthesis, respiration, nitrogen fixation, alkaline phosphatase activity, or any other process by Oscillatoria colonies, will be difficult. Cursory examination of a few colonies taken from the same plankton tow does not necessarily indicate the condition of the rest of the population.

Recently, we have become aware of an internal report from the Ocean Research Institute of the University of Tokyo. Written in Japanese and edited by Ryuzo Marumo, passing mention is made of some similar associations in clumps of decaying Oscillatoria. Thus it appears that the phenomenon we report here is widespread and might be of considerable importance.

Oscillatoria colonies are one of the most abundant forms of particulate matter in tropical seas. Similar to other particles such as organic aggregates (Riley, 1963), mucus structures (Aldredge, 1972), and Foraminifera (Aldredge, 1973), Oscillatoria constitutes a substrate for colonization by many micro-organisms. Pelagic microhabitats such as these with heterogeneous communities of associated organisms are important when considering the diversity of the plankton in open water.

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FISHERIES AND AQUACULTURE OF THE CONCH, STROMBUS GIGAS IN THE CARIBBEAN

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Abstract

The large marine snail *Strombus gigas*, known variously in different localities as the conch, botuto, cobo or lambi, supports an active fishery throughout the Caribbean. Because of extensive overfishing around nearly every island, the supply of conch is diminishing rapidly. This is evident in the taking of juvenile animals. Realizing the economic importance of the native conch fisheries, a study of the animals' relative abundance, growth and aquaculture was initiated.

Data on the growth of *S. gigas* were obtained from animals reared in aquaculture systems and from field tag-recapture experiments. Using the von Bertalanffy growth equation, we estimate that one, two and three-year old animals are 10.8, 17.0 and 20.5 cm respectively. Animals reach the flaring-lip stage after 3 years and have a mean longevity of a further 3 years.

Strombus gigas veligers have been reared through metamorphosis and as juveniles in the laboratory. Veligers hatched from egg cases within 5 days after the egg cases were laid. They were reared in 400-600 l tanks by being fed a diet of natural phytoplankton maintained at dense concentrations (10^5 cells/ml) by nutrient enrichment. The veligers metamorphosed into a crawling juvenile stage 27 to 35 days after hatching. Juveniles are being reared on algae growing on the sides of the tanks. Maximum growth rate measured to date is 0.34 mm/day. Plans are being developed for intensive culture and extensive seeding of juvenile snails at Los Roques, Venezuela.

Resumen

El caracol marino de gran talla *Strombus gigas*, conocido según las zonas con diversos nombres (botuto, conch, cobo o lambi) da vida a una activa pesquería en todo el Mar Caribe. A causa de la explotación excesiva en torno a la mayoría de las islas, las poblaciones de botuto están disminuyendo rápidamente, como lo demuestra el aumento de las capturas de moluscos juveniles. Dada la importancia económica de esta pesquería, se ha iniciado un estudio sobre la abundancia relativa, el crecimiento y el cultivo de este molusco.

Los datos sobre el crecimiento de *S. gigas* proceden de animales criados en sistemas de acuicultura y en su ambiente natural (marcado-recaptura). Utilizando la ecuación de crecimiento de von Bertalanffy, se estima que los animales de 1, 2 y 3 años tienen, respectivamente, 10,8; 17,0 y 20,5 cm. A los tres años se forma el labio grande de la concha y el botuto vive aún otros tres años por término medio.

Se ha conseguido criar en laboratorio larvas velígeras de *Strombus gigas*, que han alcanzado la metamórfosis y han pasado a la fase juvenil. Las larvas salieron del huevo a los cinco días del desove, y se criaron en tanques de 400-600 litros, alimentándose con una dieta de fitoplancton natural mantenida a concentraciones densas (10^5 células/ml) gracias a la adición de nutrientes. Las larvas se metamorfosearon, pasando a la fase juvenil, de 27 a 35 días después de la eclosión. Las formas juveniles se alimentan de algas que crecen en los costados de los tanques. El índice máximo de crecimiento encontrado hasta la fecha es de 0,34 mm/día. Se están preparando sistemas para el cultivo intensivo y la siembra extensiva de formas juveniles en Los Roques, Venezuela.

1. FISHERIES

Strombus gigas, a large marine gastropod common throughout the Caribbean, is one of the principal fisheries resources in the region. The meat is consumed on all the islands and is known variously in different localities as conch, lambi, botuto or cobo. The animals are most commonly collected on shallow grass beds associated with coral islands, either by diving for them in depths up to 10 m, or by hooking them with poles from a boat. A good conch diver can gather 600 animals in four hours of diving in depths of 1-5 m. The animals are usually removed from the shells in the field and carried to market in fishing boats.

Most conch caught are used for local consumption; however, there is a large export fishery in Belize. The Turks and Caicos Islands provide as many as 3 million conchs to markets in the U.S.A. (Hesse, 1975). Conchs from Los Roques and Las Aves are marketed in Venezuela and Curaçao. Annual catch data for the Caribbean islands are scarce and, usually, unreliable.

There are pre-Colombian archeological sites composed primarily of conch shells on many islands; conchs were a major element in the diet of Caribbean Indians. Although conchs have always been fished for food, their shells now are valued as curios and for a variety of other uses (Boss, 1969).

In recent years there has been a marked decline in the abundance of S. gigas throughout the Caribbean. This is evidenced by the fact that fishermen have resorted to taking smaller-sized animals from less-accessible areas and by decreases in the reported catches from Venezuela (Fig. 1). Many island fisheries are already severely threatened, e.g. Puerto Rico, Bahamas and Grenadines (Adams, 1970). It is important, therefore, to understand the dynamics of the conch fisheries, the effects of conch exploitation and the time it takes depeleted stocks to recuperate.

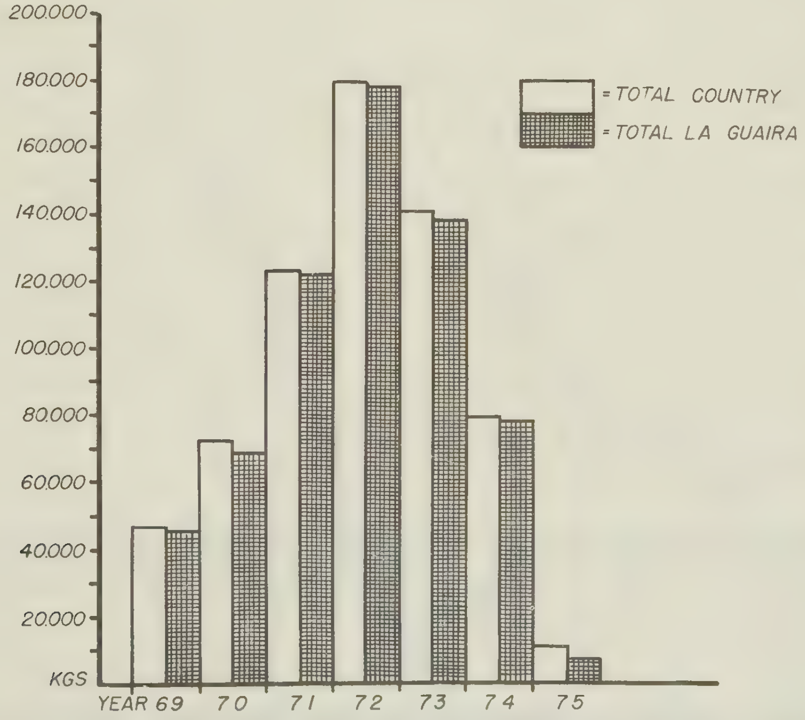

Fig. 1 Annual reported catches of Strombus gigas in Venezuela
Data from La Oficina Nacional de Pesca, Caracas

2. REPRODUCTION AND GROWTH

Knowledge of conch recuuitment, growth and mortality rates is essential for proper management of this resource. Therefore, studies of reproduction, larval life, metamorphosis and growth of juveniles were initiated in Los Roques to supplement previous information (Randall, 1964; Berg, 1976). Calculations were made on the actual growth of juveniles in the laboratory and statistical analyses were applied to data from natural conch populations.

Strombus gigas was raised in the Los Roques laboratory from eggs, through metamorphosis, and as juveniles, the oldest of which are presently ten months old and approximately 7 cm long. Maximum growth rate was 0.34 mm/day (Fig. 2). If this growth rate could be maintained, an individual would attain a length of 12 cm in one year. Growth rates for animals in their second and third years were obtained from conchs maintained in a culture system on St. Croix; these animals increased in length 7.3 cm (MD_{50}) in two years. Maximum increase was 10.9 cm (Fig. 3).

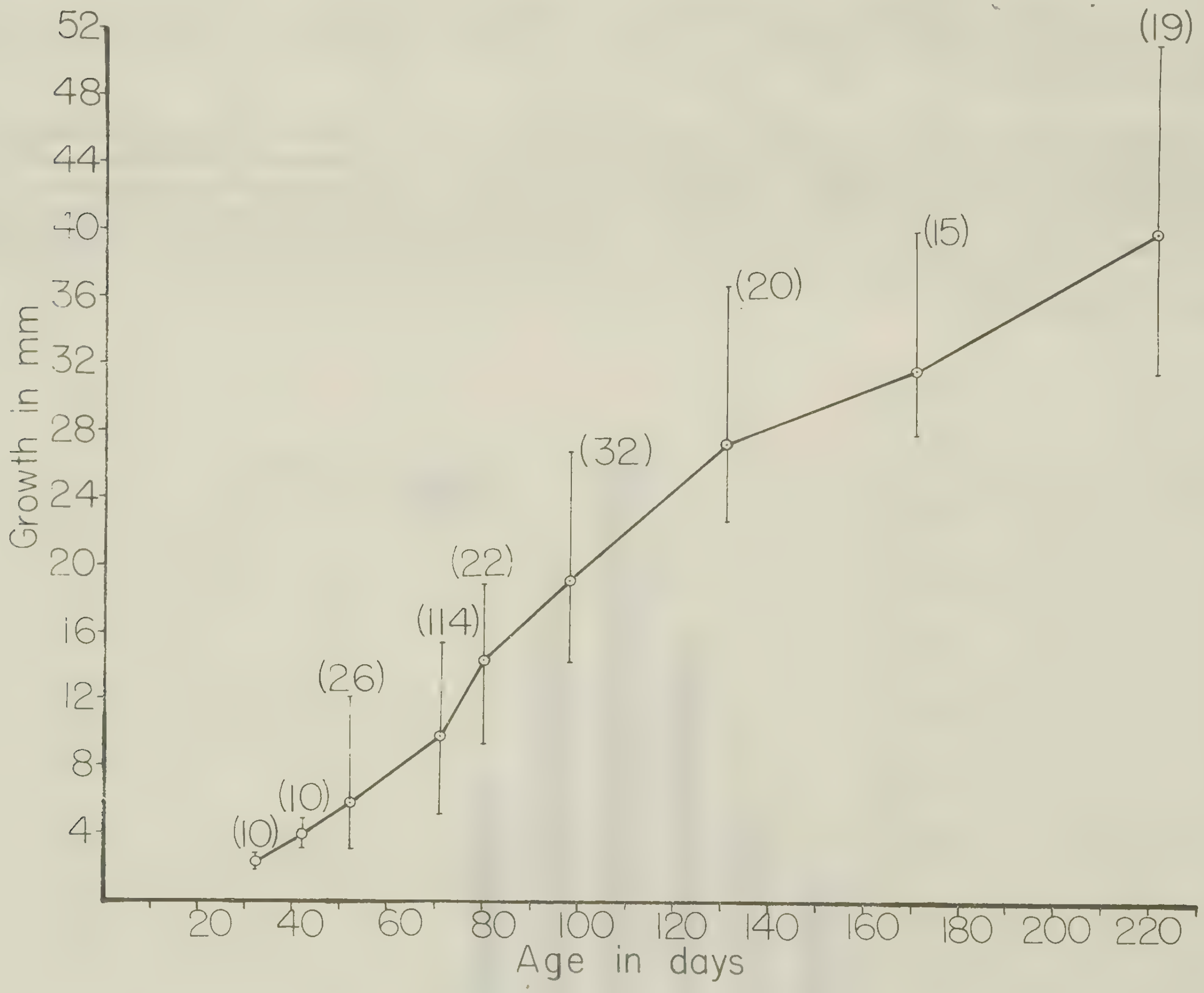

Fig. 2 Growth of Strombus gigas juveniles reared in the laboratory on Los Roques, Venezuela
(Numbers in parentheses indicate sample sizes)

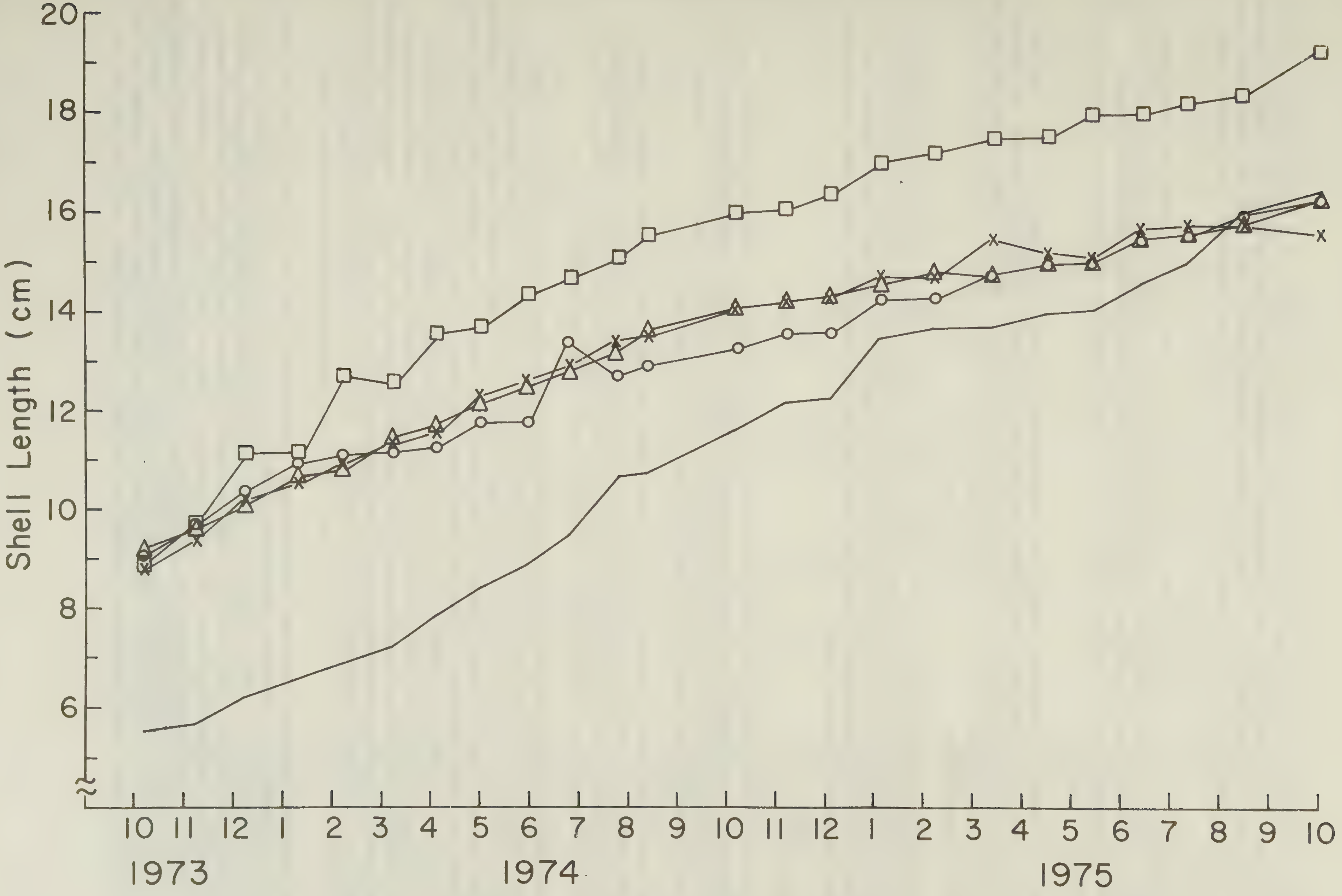

Fig. 3 Growth curves of 5 juvenile Strombus gigas reared in an aquaculture system at St. Croix, U.S. Virgin Islands

The growth rates were further substantiated by probit analysis of a population collected in Los Roques during July 1976; this population separated into size classes with mean lengths of 7.6, 12.8 and 18.0 cm (Fig. 4). These represent approximately one, two and three-year age classes and are similar in size classes of 8.8, 12.6 and 18.0 cm reported from Puerto Rico (Berg, 1976).

Application of the von Bertalanffy growth equation to 104 conchs marked and recaptured by Randall (1964) on St. John, U.S. Virgin Islands, predicts yearly mean sizes of 10.8, 17.0 and 20.5 cm for the first three years (Fig. 5). Growth curves derived from laboratory (St. Croix) animals predict a faster initial growth, but a smaller maximum size than the natural population studied.

Both estimates of juvenile growth and measurements of adult S. gigas with the flaring shell lip (Berg, 1976) indicate that sexual maturity and cessation of shell growth is reached when animals are approximately 20.4 cm long and three years old. Adult animals from Los Roques have a mean shell length of 19.8 cm (N=60). Mean longevity of adult snails is predicted to be 6-7 years (Berg, 1976).

From Fig. 6 the meat yield can be predicted from either shell length or total weight. A marketable animals of 100 g would be approximately 19 cm long, with a total weight of 850 g, and would be 2½ years old. The time required to rear marketable animals would appear to favour seeding laboratory-reared juveniles into natural environments rather than continuous laboratory culture to market size.

3. AQUACULTURE

We have reared successfully the queen conch S. gigas (as well as the related species S. pugilus and S. costatus) from eggs, through metamorphosis, into juveniles (Brownell, in press). Egg masses were collected from under the lip of females spawning in the natural environment; this assured positive indentification of the species.

Egg cases were taken directly to the laboratory and placed in 35 litre aquaria with unfiltered seawater. Veliger larvae hatched 5 days after they were laid. Egg masses and early veligers have been described by Robertson (1959) and D'Asaro (1965). "Hatchability" was always high, as was survival during the first three days of larval life.

Within 24 hours from hatching the veligers were transferred into 400-600 litre tanks containing seawater filtered through 153 µm mesh sieves. Optimum density was approximately 10 veligers per litre. Since the laboratory had no system for continuous aeration of rearing tanks, the animals were fed and aerated by replacing one third of the volume daily with natural cultures of phytoplankton. These cultures were prepared by pumping filtered seawater (153 µm mesh) into elevated fibreglass tanks and enriching the seawater to yield levels of $NaNO_3$, Na_2HPO_4, $Na_2SiO_3 \cdot 9H_2O$ and vitamins B_1 and B_{12} equivalent to one fiftieth the concentrations of these nutrients in enrichment "f" (Guillard and Ryther, 1962). Trace metals were supplied by addition of a commercial, water-soluble fertilizer (Stern's Miracid, from Stern's Nurseries, Inc., Geneva, New York 14456) at the rate of 0.332 mg per litre of seawater. Stern's Miracid contains the trace metal chelator ethylenediaminetetraacetic acid (EDTA).

The enriched seawater cultures yielded algal densitites of up to 1×10^5 cells /ml after 60-72 hours incubation. Cultures were maintained at high densities for up to 8 days by draining off 40 percent of the culture to the larvae tanks and adding back filtered seawater plus nutrient enrichment. The culture tanks received filtered sunlight (the roof was translucent fibreglass) and were aerated 6-7 hours per day. Due to the low level of enrichment used, carbon-dioxide limitation was not a problem. Some of the most common organisms observed in these cultures were Chaetoceros spp., Nitzschia spp. and Skeletonema costatum. Attempts to maintain monocultures of high temperature clones of diatoms and flagellates, as raised at the St. Croix Laboratory, were unsuccessful, due to the lack of appropriate culture facilities.

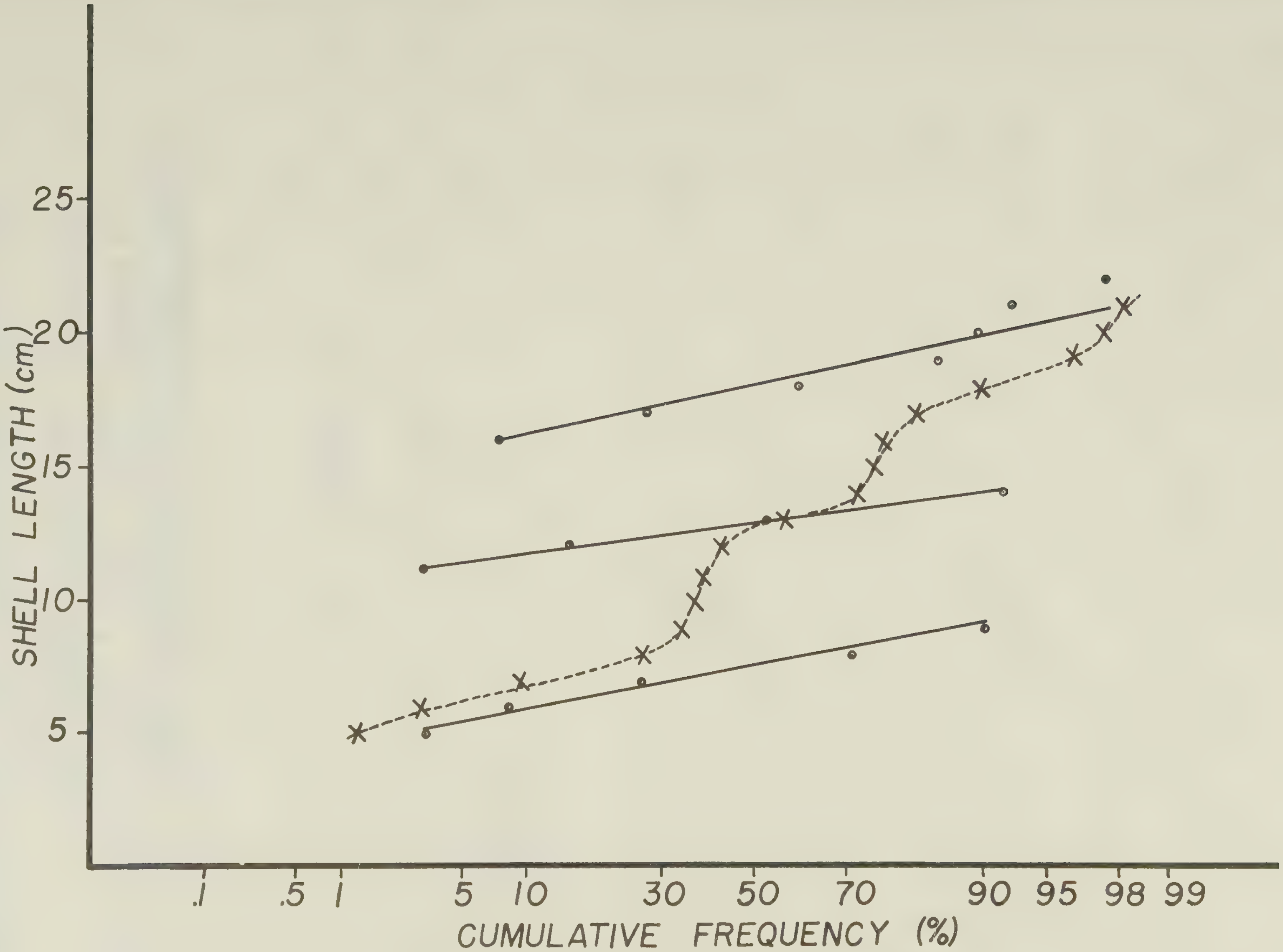

Fig. 4 Probit distribution of shell lengths of 161 juvenile *Strombus gigas* collected at Los Roques on 19 July and 20 July 1976. Crosses = total sample; filled circles = sub-samples

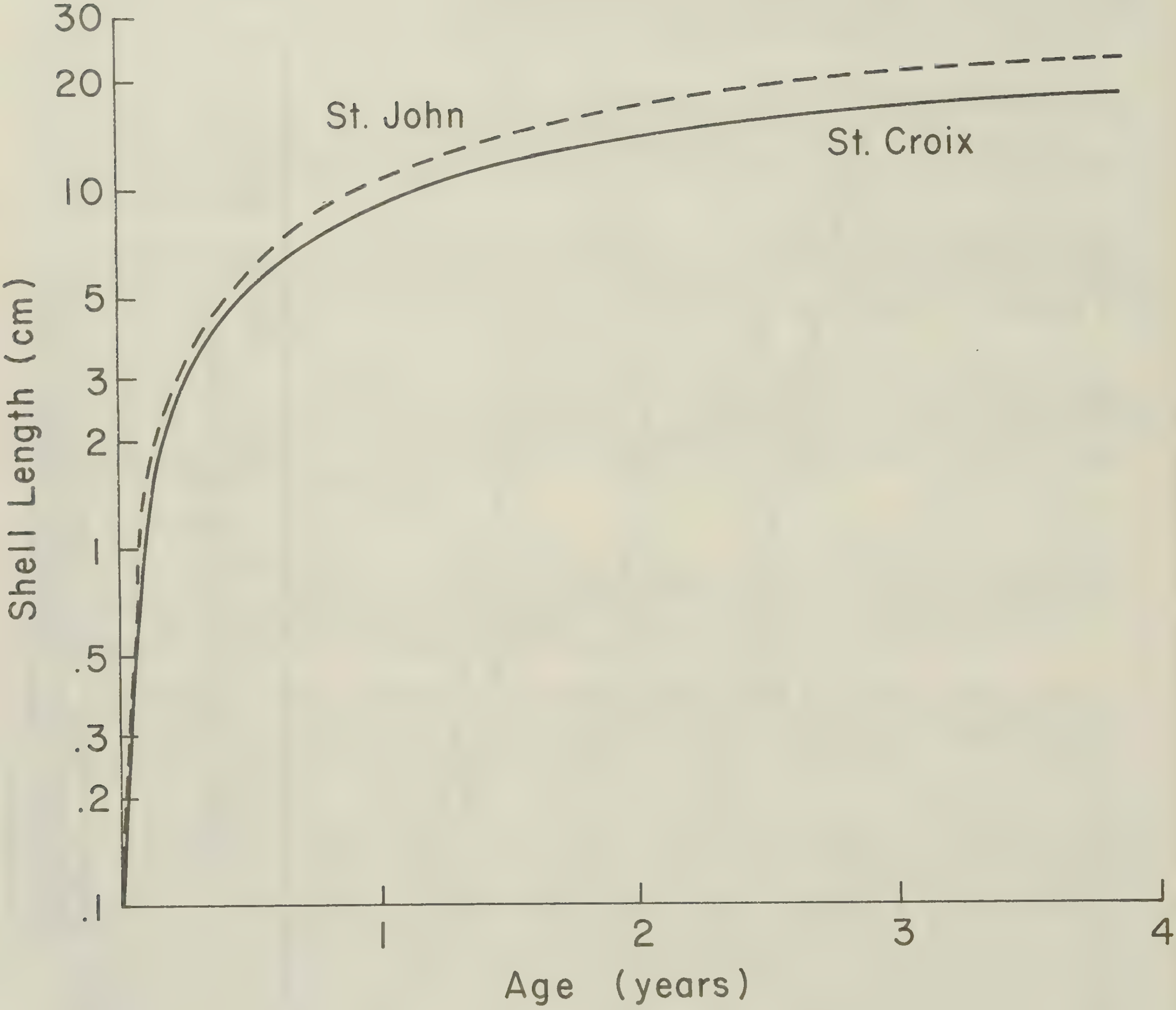

Fig. 5 Von Bertalanffy growth curves for Strombus gigas fitted to data from Randall (1964) and from snails reared for 2 years in an aquaculture system on St. Croix

St. John: $L_t = 260.4\ (1-0.99539\ e^{-0.0014135\ t})$

St. Croix: $L_t = 200.79\ (1-0.99402\ e^{-0.0016136\ t})$

(after Berg, 1976)

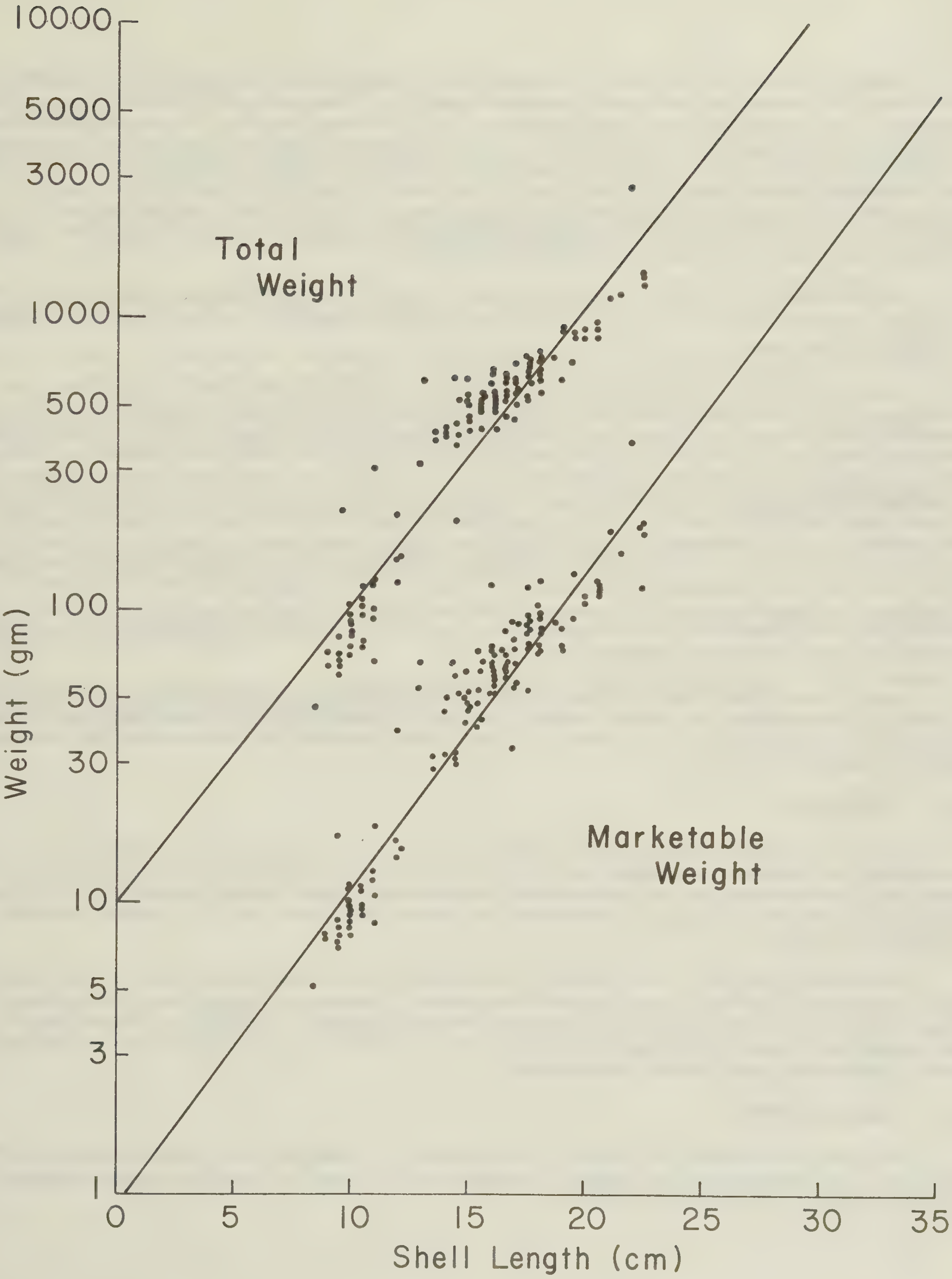

Fig. 6 Correlation between maximum shell length of 129 juvenile *Strombus gigas* and both total weight and marketable meat weight. Log_{10} total weight = 1.003 + 0.102 shell length, r = 0.94. Log_{10} market weight = 0.045 + 0.109 shell length, r = 0.95 (from Berg, 1976)

A major problem in the culture process was the unavoidable introduction of predators, especially copepods, in the form of eggs and nauplii. These were filtered out only at the expense of excluding important phytoplankton. A filter mesh size of 120 µm eliminated most predators and, apparently, excluded only the phytoplankton that are consumed by the advanced stages of veligers. One of our most successful batches of animals resulted from feeding fine phytoplankton (using water filtered with 103 µm mesh) during the first week and larger organisms (202 µm mesh) during the remaining 12 days of the swimming veliger stage. In this way copepod nauplii entering through the coarsely filtered water reached adult size only after veligers were large and approaching metamorphosis.

Temperatures in hatchery tanks during key stages of larval-juvenile development of S. gigas ranged from 23.8°C to 29.6°C between July and February. Salinity ranged from 34‰ to 37‰ in the tanks.

Development of the veligers from pre-hatching to pre-metamorphosis is described by D'Asaro (1965). The embryo develops within the egg capsule for approximately 5 days and then pushes its way out of the capsule through an "escape hatch" (D'Asaro, 1965). Newly emerged veligers have two minute velar lobes which are employed immediately for swimming to the surface. These lobes begin to divide into four by the fifth day after hatching and become active food-gathering as well as swimming mechanisms. By the eighth day the anterior pair of velar lobes begin to divide again. Veligers continue to swim and feed near the surface until approximately the nineteenth day, although they often spend brief periods at, or near, the bottom in the interim. Veligers were observed crawling on the sides of tanks on the twentieth day, but they were principally planktonic at that time. Metamorphosis occurs between 27 to 35 days after hatching. In all cases, juveniles were only feeding on films of algae coating the sides of the tanks by the thirtyfifth day and the velar lobes had disappeared completely. Juvenile growth rates are presented in Fig. 2.

Larval development can be slowed appreciably by inadequate diet, but the veligers are capable of subsisting for several weeks on a bare minimum of proper planktonic food. However, after a prolonged period of malnutrition, they seem incapable of recuperating and metamorphosing (D'Asaro, 1965).

4. CONCLUSIONS

Given the great economic and nutritive importance of conchs in the Caribbean, it is necessary to establish management and aquaculture practices that will assure continued production of this resource. Existing conch fisheries are under intense pressure. This has resulted in underutilization of extensive sea grass beds, which are the primary feeding grounds for conchs.

Due to the naturally slow growth of this species, it seems impractical at this time to rear the animals entirely in an aquaculture system. However, S. gigas could be raised in the laboratory through the period ofgreatest susceptibility to predation. Juveniles of 3-4 cm in length could then be released on natural shallow grass flats for either re-establishment of wild populations or extensive aquaculture.

5. ACKNOWLEDGEMENTS

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SIGNIFICANCE OF N_2 FIXATION TO THE PRODUCTION OF THALASSIA TESTUDINUM COMMUNITIES

by

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Abstract

N_2 fixation (C_2H_2 reduction) associated with the leaves, root system and rhizosphere sediments of *T. testudinum* was assayed at sites in Biscayne Bay (Florida) and Bimini Harbor (Bahamas). Activities in the phyllosphere were low except where a heterocystous blue-green alga (*Calothrix* sp.) occurred. Bacterial contributions on the leaves were negligible because organic compounds and anaerobic conditions did not stimulate N_2 fixation. Where *Calothrix* sp. was present a seasonal variation in activity was evident and the fixation during the summer amounted to between 4 and 23% of the daily nitrogen requirement for established grass beds. N_2 fixation was higher at the periphery of a grass patch, amounting to between 8 and 38% of the required nitrogen, perhaps reflecting a less efficient recycling of nitrogen in such regions. Washed roots and rhizomes had low activities, with lag periods of 12-18 h before C_2H_2 reduction commenced. Glucose stimulated C_2H_2 reduction in these systems but neither glucose nor anaerobic conditions eliminated the lag phase. Sediments incubated anaerobically in the dark, with or without root systems, catalyzed C_2H_2 reduction with negligible or very short lag periods (1-2 h). The activity was stimulated by glucose and was also detectable to depths of 40 cm in the sediments. Estimated annual inputs varied considerably but were usually in the range of 50-100 KgN ha^{-1} y^{-1} N_2 fixation associated with the phyllosphere, in our study area, was highly variable, both spatially and temporally, but was significant at some sites. Bacterial N_2 fixation in the sediments, however, is probably sufficient to account for the high productivities of *T. testudinum* in the nutrient-poor waters of the localities examined.

Resumen

En algunas zonas de la bahía de Biscayne (Florida) y la isla de Bimini (Bahamas) se ha estudiado la fijación de N_2 (reducción de C_2H_2) en las hojas, el sistema radical y el substrato de *T. testudinum*. La actividad de fijación en las hojas fue relativamente baja, excepto cuando se encontraba como epifito el alga verde-azul (con heterocisto) *Calothrix* sp. La contribución de las bacterias presentes en las hojas resultó insignificante, porque

los compuestos orgánicos y las condiciones anaeróbicas no estimularon la fijación de N_2. En los casos en que aparecía Calothrix sp. se observó una variación estacional en la actividad: durante el verano, la fijación ascendió a entre 4 y 23% de las necesidades diarias de nitrógeno de las comunidades establecidas. La fijación de N_2 resultó mayor en la periferia de la comunidad, ascendiendo a entre 8 y 38% del nitrógeno necesario, debido quizás a un reciclaje menos eficiente del nitrógeno en esas regiones. En raíces y rizomas lavados se observó baja actividad, con períodos de retraso de 12-18 horas antes del comienzo de la reducción de C_2H_2. Se halló que la glucosa estimula la reducción de C_2H_2 en esos sistemas, pero ni la glucosa ni las condiciones anaeróbicas reducen el período de retardo. En sedimentos incubados anaeróbicamente en la oscuridad, con o sin sistema radical, se produjo reducción de C_2H_2 con períodos de retardo insignificantes o muy breves (1-2 h). Se halló que la glucosa estimula la actividad, que pudo detectarse a profundidades de 40 cm en los sedimentos. Los valores calculados de N_2 fijado variaron considerablemente, pero fueron en general del orden de 50-100 KgN ha^{-1} $año^{-1}$. La fijación de N_2 asociada con las hojas en la zona en que hicimos nuestro estudio, resultó muy variable, tanto espacial como temporalmente, pero en algunos lugares fue importante. De todas formas, probablemente la fijación bacteriana de N_2 en los sedimentos es suficiente para explicar la alta productividad de T. testudinum en las aguas pobres en nutrientes de las zonas examinadas.

1. INTRODUCTION

Sea grasses grow in shallow marine waters and Thalassia testudinum (turtle grass) is the most abundant in Biscayne Bay, Florida Keys, Gulf of Mexico and Caribbean region (Humm, 1964). Subtropical and tropical marine waters are often deficient in nutrients (Smith, Williams and Davis, 1950; Zuberer and Silver, 1975) but, even so, the production rates of T. testudinum rank amongst the highest known (Westlake, 1963). Patriquin (1972) found, for communities of T. testudinum growing in coastal regions near Barbados, the sediments contained adequate reserves of phosphorus, but not nitrogen. He suggested therefore that nitrogen in the sediments was replenished by the activities of N_2 fixing bacteria. This idea was supported by the subsequent detection of high rates of C_2H_2 reduction associated with the rhizomes and rhizosphere sediments of T. testudinum (Patriquin and Knowles, 1972). C_2H_2 reducing activity has also been attributed to colonies of heterocystous blue-green algae (e.g. Calothrix sp.) in the phyllosphere of T. testudinum in Redfish Bay, Texas (Goering and Parker, 1972). The N_2 fixed by the epiphytic Calothrix sp., if available to the macrophyte, easily accounted for the observed production rates of sea grass flats in Redfish Bay (Goering and Parker, 1972; Odum and Hoskins, 1958). However, more recent work has questioned the general occurrence of N_2 fixation both in the rhizosphere and phyllosphere of sea grasses (McRoy, Goering and Chaney, 1973). Our objective, therefore, was to investigate the occurrence and significance of N_2 fixation associated with communities of T. testudinum growing in Biscayne Bay (Florida) and nearby regions.

2. METHODS

N_2 fixation was assayed by C_2H_2 reduction (Stewart, Fitzgerald and Burris, 1967); C_2H_2 and C_2H_4 were measured by gas chromatography (Bunt et al., 1970). A molar ratio of 3:1 was used to convert C_2H_4 production to N_2 fixed (Hardy et al., 1968). Our procedures for determining C_2H_2 reduction associated with the phyllosphere have been described (Capone and Taylor, 1977). Samples of roots, rhizomes and sediments were collected using aluminium cores (diameter, 7.5 cm). The C_2H_2 reduction assays were conducted in either serum bottles or Erlenmeyer flasks, incubated in the dark at 26°C or 30°C, usually with gentle reciprocal shaking. The gas phase was either air or an anaerobic gas (N_2, He, or Ar) containing 10% or 20% C_2H_2. Anaerobic gases were freed from traces of O_2 by passage through a glass column containing hot copper wire (Hungate, 1969). Isolated roots and rhizomes were rinsed in seawater prior to assay and the rhizomes cut into sections about 2-4 mm thick. In some experiments the sediments were diluted, in the assay vessels, with an equal volume of seawater (previously deoxygenated by boiling and purging with an O_2-free gas in anaerobic experiments). In other experiments the sediments were added to an equal volume of deoxygenated seawater contained in a Waring blender and then gently homogenized. The blender was continuously flushed with an O_2-free gas during homogenization and precautions taken to exclude air (Hungate, 1969) during subsequent transfer of the sediment slurry to the assay vessels.

Investigations into the distribution of C_2H_2 reduction with depth in the sediments were carried out using a plexiglass tube, length 80 cm, diameter 7.5 cm, having 16 mm diameter holes along its vertical axis. These holes were sealed with air conditioning tape before driving the tube into the sediment. The upper end of the tube was then sealed with a rubber stopper containing a pressure relief valve. The valve consisted of a pinch clamp on a piece of rubber hose attached to a short steel tube which pierced the rubber stopper. After closing this valve, the core was removed from the sediment and a rubber stopper inserted into the lower end of the tube (during this operation the pressure relief valve was opened briefly. The sediment column was then returned to the laboratory or the R/V CALANUS. After removing the air conditioning tape, samples of sediment were removed from the column using cut-off plastic syringes. These portions of sediment (volumes about 5 ml) were assayed separately for C_2H_2 reduction in Erlenmeyer flasks (volume 30 ml) containing 5 ml of deoxygenated seawater and a gas phase of 10% or 20% C_2H_2 in argon. Aluminium tubes (length, 5 cm) bearing rubber O-rings were inserted into the holes in the plexiglass tube, and then sealed with serum caps. After flushing each space with argon containing 10%

or 20% C_2H_2, the entire column was incubated in the dark at ambient temperature (usually about 26°C) in a water-bath.

C_2H_4 production was related to dry weight of sediments (75°C) or root material (105°C)

3. RESULTS

3.1 N_2 Fixation in the Phyllosphere

Our primary region of study is shown in Fig. 1. Some experiments were also carried out in the grass flats in Bimini Harbor. Characteristics of the sites and results of our work on N_2 fixation in the phyllosphere are described in detail in a recent paper (Capone and Taylor, 1977). Appreciable activities were detected only at Stations 2 (Soldier Key) and 5 (Fowey Rock), and in Bimini Harbor. Colonies of a Calothrix sp. were evident on the leaves and heterocystous blue-green algae were the organisms principally active in C_2H_2 reduction at these three sites. This conclusion was supported by results from experiments on diurnal variation in activity and lack of stimulation of C_2H_2 reduction by organic additions (e.g. glucose) under either aerobic or anaerobic conditions in the light or dark (Capone and Taylor, 1976). Annually, the amount of N_2 fixed at Station 5 (Fowey Rock) was about 5 KgN ha^{-1} and about 0.1 KgN ha^{-1} at Station 2 (Soldier Key) (Table I). N_2 fixation, associated with leaves, was negligible at the other stations in Biscayne Bay. N_2 fixation in the phyllosphere was also evaluated on a daily basis from the results obtained in the summer months at Fowey Rock and in Bimini Harbor (Table I). In these calculations, leaf standing stocks of 200 g dry weight m^{-2} were assumed and a nitrogen content of 0.9% of dry weight for dead leaves (Capone and Taylor, 1977). Leaf productivities, using the data of Wood, Odum and Zieman (1969) for communities of T. testudinum in Biscayne Bay, were assumed to fall in the range of 2.2 to 10 g dry weight m^{-2} day^{-1}. Accordingly, N_2 fixed constituted 4-19% at Station 5, and 5-23% of the daily nitrogen required for leaf production in Bimini Harbor (Table I). C_2H_2 reduction was also examined at Fowey Rock with respect to location of the plants within a community (Capone and Taylor, 1977). Results from such a transect experiment are summarized in Table II. In these calculations the production data of Wood, Odum and Zieman (1969) were adjusted in accord with the measured leaf standing stocks (i.e. a production of 1.1-5.0% of the standing stock per day). N_2 fixation in the centre of the grass patch could provide 3-13% of the estimated daily requirement for leaf production (Table II). In contrast, at the fringe of the grass bed, the total N_2 fixed per square metre is similar, but constitutes 8-38% of the daily requirement because of the smaller standing stocks of leaves (Table II).

3.2 N_2 Fixation in the Rhizosphere

Washed roots and rhizomes catalyzed the reduction of C_2H_2 to C_2H_4, but only after a considerable lag period (as shown in Fig. 2 for rhizomes). Neither anaerobiosis nor the addition of glucose eliminated the lag phase, but glucose did increase the rate of C_2H_2 reduction attained after the initial lag.

Several experiments were carried out with plexiglass incubation cores (see METHODS) to determine whether N_2 fixation, like the root system of T. testudinum, extended to significant depths within the sediments of the grass beds. The results of one such experiment, using material from Station 2 (Soldier Key), are illustrated in Figure 3. C_2H_4 was produced (only in the presence of C_2H_2) within the gas spaces of the horizontal aluminium cores in the sediment, and its concentration increased with time. Similar experiments were performed with sediment columns obtained from beds of T. testudinum at Caesar Creek (South Biscayne Bay) and in Bimini Harbor; C_2H_2 reduction in these localities proceeded at depths of at least 39 cm and 29 cm, respectively. The assays in small Erlenmeyer flasks on material removed from the sediment column, conducted in parallel with the plexiglass core incubations, gave similar results. The overall picture which emerged from these qualitative experiments was that C_2H_2 reduction did occur at appreciable depths within the sediments

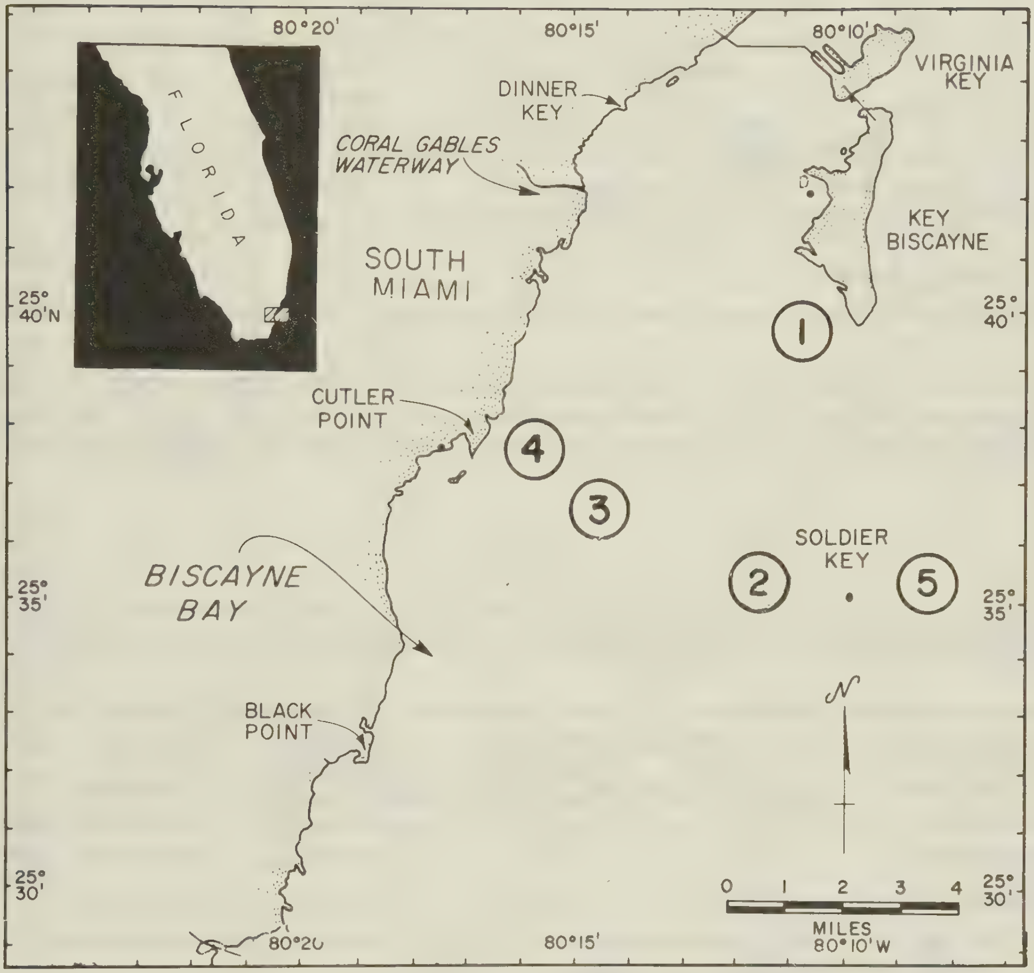
80°20'
80°15'
80°10'
VIRGINIA KEY
DINNER KEY
CORAL GABLES WATERWAY
FLORIDA
KEY BISCAYNE
SOUTH MIAMI
25° 40'N
25° 40'
1
CUTLER POINT
4
3
SOLDIER KEY
2
5
BISCAYNE BAY
25° 35'
25° 35'
N
BLACK POINT
0 1 2 3 4
MILES
25° 30'
25° 30'
80°20
80°15'
80°10'W

Fig. 1 Map showing the locations of the stations primarily employed to investigate N_2 fixation associated with Thalassia testudinum

TABLE I

Significance of N_2 fixation in the phyllosphere of *Thalassia testudinum* in relation to nitrogen required for leaf production

Station	Annual N_2 fixation ($KgN\ ha^{-1}$)	Daily N_2 fixation ($mgN\ m^{-2}$)	Nitrogen required[a] ($mgN\ m^{-2}day^{-1}$)	N fixed: N required
5 (Fowey Rock)	5	3.8	20-90	0.04-0.19
2 (Soldier Key)	0.1	-	-	-
Bimini Harbor	-	4.6	20-90	0.05-0.23

a/ Calculated on the basis of a nitrogen content of 0.9% of dry weight for dead leaves (Capone and Taylor, 1976), leaf standing stocks of 200 g dry wt m^{-2} and leaf production rates of 2.2-10 g dry wt m^{-2} day^{-1} (Wood, Odum and Zieman 1969)

TABLE II

Variation of N_2 fixation in the phyllosphere at the fringe and centre of a bed of *Thalassia testudinum* and its relationship to nitrogen required for leaf production[a]

Location in grass bed	Leaf standing stocks (g dry wt m^{-2})	Daily N_2 fixation ($mgN\ m^{-2}$)	Nitrogen required[b] ($mgN\ m^{-2}day^{-1}$)	N fixed: N required
Periphery	43	1.6	4.2-19	0.08-0.38
Centre	164	2.0	16-74	0.03-0.13

a/ Experiments performed at Station 5 (Fowey Rock)

b/ Calculated on the basis of a nitrogen content of 0.9% of dry weight for dead leaves (Capone and Taylor, 1976) and the leaf production rates of Wood, Odum and Zieman (1969) adjusted in relation to measured leaf standing stocks (i.e. 1.1-5.0% of standing stock produced per day)

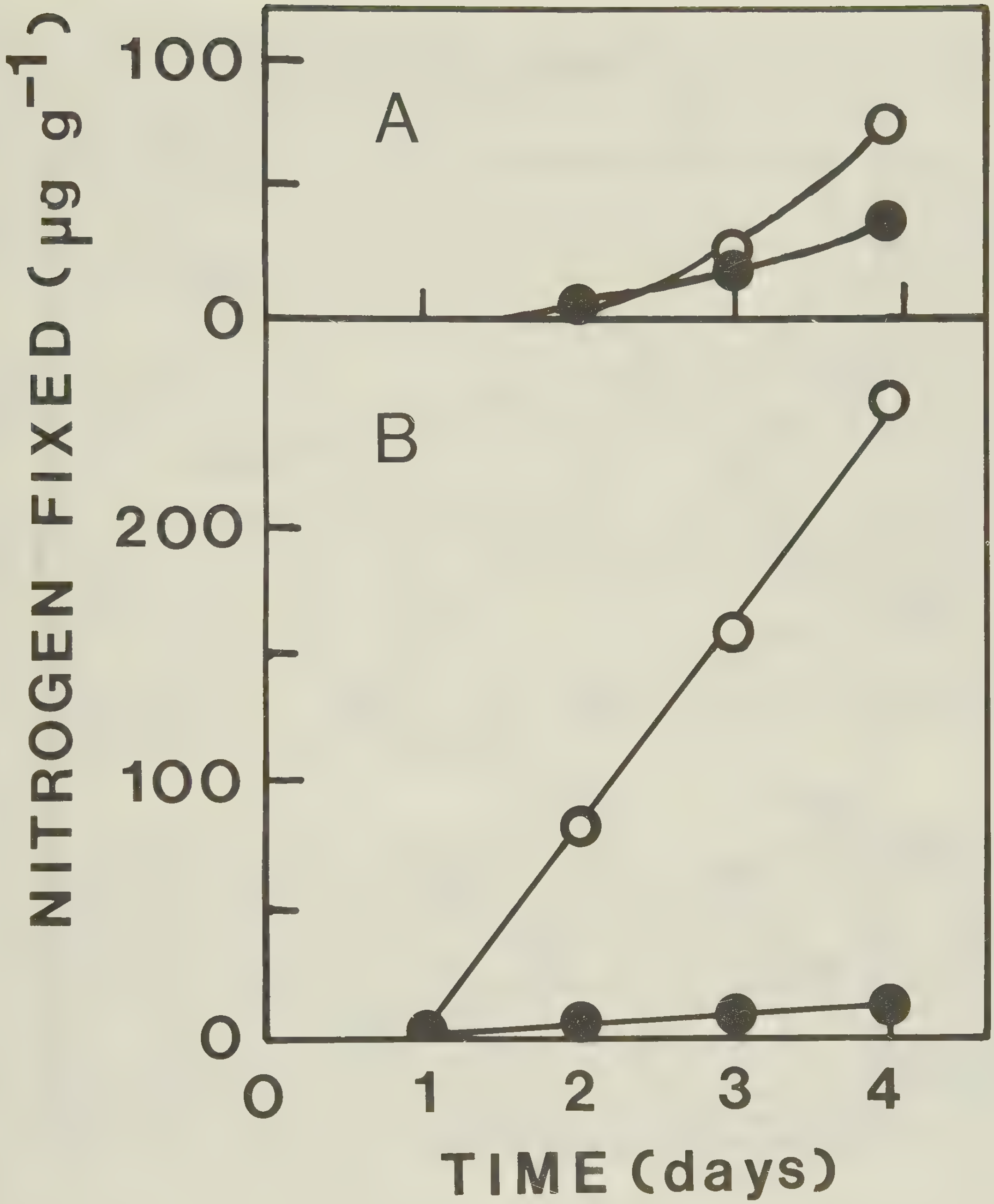

Fig. 2 N_2 fixation associated with rhizomes of Thalassia testudinum obtained from grass beds in Bimini Harbor. The rhizome slices were assayed in 70 ml serum bottles containing 15 ml of seawater with 10% C_2H_2 in the gas phase. The bottles were incubated, with reciprocal shaking, at 26°C in the dark and contained between 0.21 to 0.45 g dry wt of rhizome tissue. N_2 fixation rates are expressed as µgN fixed per g dry wt of rhizome tissue

Symbols: A, aerobic; B, anaerobic (argon); O, 5mM glucose; O, no glucose

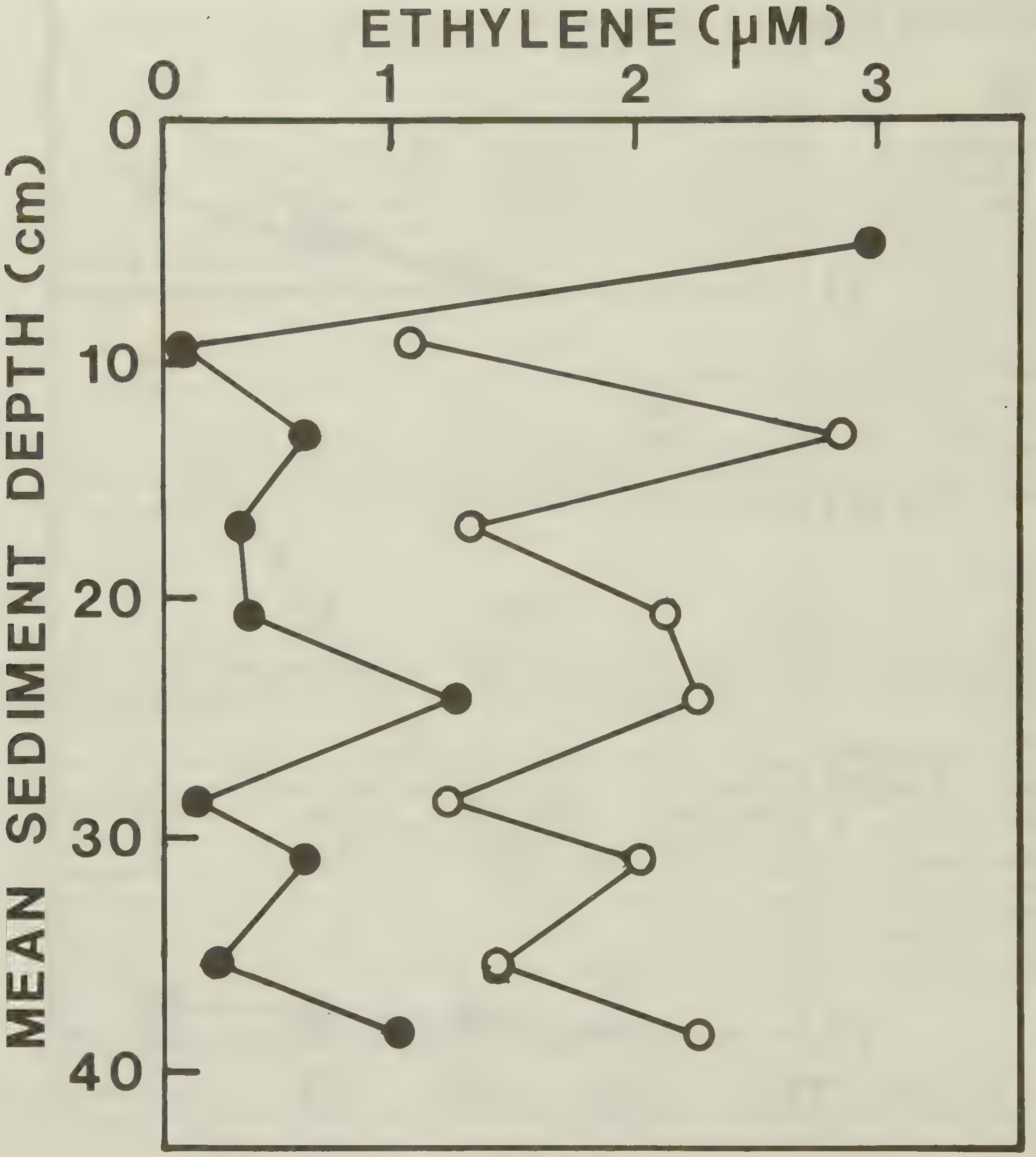

Fig. 3 Depth profile of N_2 fixation associated with a column of sediment obtained from a bed of Thalassia testudinum at Soldier Key (Station 2). A plexiglass incubation core was used in this experiment (see METHODS). The concentration of C_2H_4 in the gas in the horizontal aluminium tubes is shown after 4 hours (●) and 24 hours (O)

of communities of T. testudinum, but the higher activities were concentrated in the upper sediment layers. A more thorough study was therefore undertaken with rhizosphere sediments collected at Soldier Key, to determine the quantitative distribution of N_2 fixation with sediment depth. The results from three such experiments are summarized in Table III. In these investigations 10 cm sections from the top 30 cm of sediment columns were anaerobically homogenized and then portions were anaerobically assayed for C_2H_2 reduction. N_2 fixation rates were calculated from initial rates (2-6 h) of C_2H_4 production. Less than 15% of the total activity was found in the 20-30 cm fraction, the major portion of activity (45-70%) being found in the upper 10 cm. Further studies were therefore concentrated upon the upper 10 cm of the rhizosphere. Further assays were also scaled up to use increased amounts of sediment. Complete columns of the top 10 cm of sediment were added directly (except when the rhizomes and roots were first removed) to deoxygenated seawater contained in 550 ml Erlenmeyer flasks. The objectives of these modifications were to preserve the integrity of the rhizosphere systems to minimize the exposure of the microbial populations to air and to counteract variations in results due solely to the heterogeneity of distribution of N_2 fixing activity in the rhizosphere. Higher activities were indeed obtained in these assays of the top 10 cm of sediment derived from the grass beds near Soldier Key (Table IV).

Estimates of daily and annual rates of N_2 fixation for Station 2 (Soldier Key) are compiled in Table V. These projections are based on the data shown in Tables III and IV and a sediment density of 900 kg dry weight m^{-3}. Determinations of sediment densities (0-30 cm depth) gave values of about 850 and 950 kg dry weight m^{-3} in grass beds at Soldier Key and Bimini Harbor, respectively.

As a prelude to projected studies on the N_2 fixing microflora in the rhizosphere, the effects of organic substrates and molybdate on N_2 fixation were examined. Glucose and lactate stimulated C_2H_2 reduction, whereas molybdate decreased the rate of C_2H_2 reduction associated with rhizosphere sediments (Table VI).

4. DISCUSSION

Colonies of Calothrix sp. were apparent on the leaves of T. testudinum wherever C_2H_2 reduction was easily detected in the phyllosphere (i.e. at Stations 2, 5 and in Bimini Harbor). Earlier studies indicated a correlation between N_2 fixation in the phyllosphere of sea grasses and occurrence of Calothrix sp. (Goering and Parker, 1972; McRoy, Goering and Chaney, 1973). Indeed, species of this genus of heterocystous blue-green alga are often important in N_2 fixation associated with marine systems (Capone, Taylor and Taylor, 1977; Stewart, 1971; Wiebe, Johannes and Webb, 1975). The only organisms equipped to fix N_2 under fully aerobic conditions are blue-green algae possessing heterocysts (excepting Oscillatoria (Trichodesmium) sp.; Carpenter and Price, 1976); therefore the leaf environment of sea grasses probably favours their development. However, microaerophilic and anaerobic microenvironments probably do exist on the surfaces of the leaves bearing heavy growths of epiphytes, and this circumstance must be considered when studying N_2 fixation in the phyllosphere (Capone and Taylor, 1977).

Stimulation by glucose of C_2H_2 reduction, associated with either washed rhizomes or roots, is explicable in terms of an energy requirement normally met by the macrophyte in situ. The lag period observed in these systems certainly raises a question as to whether the organisms involved actually fix N_2 in situ. Roots and rhizomes used in these experiments were collected at about mid-day, when high concentrations of O_2 are present in the lacunae of the rhizomes (Oremland and Taylor, unpublished data). The nitrogenase of the microflora might therefore have been inactivated by O_2 at such times. Further work is needed to resolve the situation with respect to roots and rhizomes including diurnal studies and isolation and investigation of pure cultures. In the rhizosphere sediments, the inhibition of a significant portion of the N_2 fixing activity by molybdate implicates sulfate-respiring bacteria in the process. Molybdate inhibits the activity of adenosine triphosphate (ATP) sulfurylase (Wilson and Bandurski, 1958), a key enzyme in the dissimilatory reduction of sulfate by sulfate-respiring bacteria (Akagi and Campbell, 1962; Peck, 1959).

TABLE III

Distribution with depth of N_2 fixation associated with sediments from communities of Thalassia testudinum at Soldier Key

Sediment section[a] (cm)	N fixation[b] (μgN g dry wt^{-1}h^{-1})		
0–10	1.32 (0.19)	2.82 (0.49)	3.39 (0.51)
10–20	0.47 (0.24)	2.55 (0.34)	1.04 (0.14)
20–30	0.29 (0.13)	0.83 (0.19)	0.43 (0.17)

a/ Core sections were briefly homogenized (anaerobically) in equal volumes of deoxygenated seawater. 20 ml portions of the sediment slurries were assayed anaerobically (10% C_2H_2 in argon) in 50 ml Erlenmeyer flasks which were incubated in the dark, with reciprocal shaking, at 26°C. The flasks contained a mean of 7.9 g dry wt of sediment (standard deviation, 1.4 g)

b/ Three separate experiments conducted in consecutive weeks in May 1975. Nitrogen fixation rates were calculated from C_2H_2 reduction rates during the period of 2-6 hours after adding C_2H_2. The results shown are the means of four replicates and the standard deviations are given in parentheses

TABLE IV

N_2 fixation associated with the upper 10 cm of the rhizosphere in beds of Thalassia testudinum at Soldier Key

System assayed[a]	Biological material[b] per flask (g dry wt)	N_2 fixation[c] (μgN g dry wt^{-1}h^{-1})
Sediments, rhizomes and roots	196 (2.7)	7.49 (1.28)
Sediments, rhizomes and roots	129 (7.5)	5.26 (2.86)
Sediments	137 (10.4)	5.11 (1.31)

a/ Assays conducted on cores of the upper 10 cm of sediment which were added directly, without homogenization, to 550 ml Erlenmeyer flasks containing 200 ml of deoxygenated seawater. The gas phase (vol. about 150 ml) was 10% C_2H_2 in argon and the flasks were incubated, with reciprocal shaking, at 26°C in the dark

b/ Standard deviations in parentheses

c/ Two separate experiments performed in Oct. 1975. N_2 fixation rates were calculated from C_2H_2 reduction rates occurring 2-6 hours after adding C_2H_2. Results are the means of four replicate assays and standard deviations are given in parentheses

TABLE V

Estimates of daily and annual N_2 fixation in the rhizosphere of Thalassia testudinum at Soldier Key

		N_2 fixation	
Material assayed[a]	Depth assayed (cm)	mgN m^{-2}day^{-1}	KgN ha^{-1}y^{-1}
S	0–30	4.5	16
S	0–30	13.4	49
S	0–30	10.5	38
SR	0–10	16.2	59
SR	0–10	11.4	42
S	0–10	11.0	40

[a] S = sediment; SR = sediments plus rhizomes and roots

TABLE VI

Effect of glucose, lactate, and molybdate on N_2 fixation associated with rhizosphere sediments (Soldier Key)[a]

Addition	N_2 fixation (μgN g dry wt^{-1})			
	6 h	21 h	45 h	121 h
None	5.5	15	27	98
Glucose, 5mM	4.6	940	3 300	6 700
Lactate, 5mM	4.9	27	650	5 200
Molybdate, 20mM	3.9	10	13	31

[a] Assays were performed on homogenized sediment (collected from 0–30 cm depth) contained in 550 ml Erlenmeyer flasks. Gas phase (vol. 150 ml) was 10% C_2H_2 in He and each flask contained about 160 g (dry weight) of sediment. The organic compounds and molybdate were added at zero time with the C_2H_2. Incubation in the dark at 26°C with reciprocal shaking.

The fact that lactate, which is a universal substrate for sulfate-respiring bacteria (LeGall and Postgate, 1973), stimulated C_2H_2 reduction further indicates that these organisms are involved in N_2 fixation and rhizosphere sediments. Glucose, however, had a more immediate stimulatory effect on N_2 fixation. Only species of Desulfotomaculum, which have not yet been found in marine environments (LeGall and Postgate, 1973), can attack glucose. This fact, together with the incomplete inhibitory effect of molybdate, indicates that other physiological types of anaerobic bacteria are also important in N_2 fixation in rhizosphere sediments (Patriquin and Knowles, 1972).

N_2 fixation in the phyllosphere of T. testudinum was negligible at four out of six of our primary study sites. Even for the communities near Fowey Rock and in Bimini Harbor, the potential input from N_2 fixation only provided an apparently minor portion (4-23%) of the estimated daily requirement of nitrogen for leaf production. Our most interesting observation concerning the phyllosphere was the detection of higher C_2H_2 reduction rates associated with leaves of plants at the periphery as compared with the centre, of a grass bed near Fowey Rock. Further work is needed to determine whether this situation is common to communities of T. testudinum in which N_2 fixation in the phyllosphere is significant. Detached leaves are probably more easily swept away by currents from the peripheries of grass beds, with lower plant densities (Table II), and therefore less nitrogen is recycled within such regions. Higher rates of Phyllosphere N_2 fixation might compensate for the loss; also peripheral regions might be developing areas of the community and consequently require more nitrogen to effect a net production of new plants.

Other workers, investigating different localities, have found either very high (Patriquin and Knowles, 1972), or very low, rates of C_2H_2 reduction (McRoy, Goering and Chaney, 1973) associated with the rhizosphere sediments, rhizomes and roots of T. testudinum. Our studies of N_2 fixation in the rhizosphere were confined mainly to communities at one site. Estimates of annual rates for N_2 fixation in the upper 10 cm of the rhizosphere at Station 2 (Soldier Key) fall in the range of 40-59 KgN ha^{-1} (Table V). If these values constitute 70% of the activity present in the upper 30 cm of the rhizosphere (Table III), then the total annual inputs amount to between 60 and 84 KgN ha^{-1}. Projections from hourly to yearly rates are tenuous, particularly since seasonal variations in activity were not investigated. As might be expected with photosynthetic blue-green algae, seasonal fluctuations in the phyllosphere were significant (Capone and Taylor, 1977). Bacteria in the rhizosphere probably depend, at least in part, on energy supplied by the macrophyte and therefore some degree of variation in activity with season also might be expected. On a daily basis about 16-23 mgN m^{-2} are fixed in the rhizosphere (again assuming that the values in Table V represent 70% of the total activity in the sediment column). This input amounts to between 16% and 116% of the estimated daily requirement of nitrogen for leaf production (Table I). In other words, N_2 fixation in the rhizosphere could provide a significant portion, or even all, the nitrogen needed for leaf production in communities of T. testudinum near Soldier Key. This conclusion lends support to the concept of Patriquin (1972) concerning the origin of nitrogen necessary for development of sea grass communities.

5. CONCLUSIONS

The quantitative significance of N_2 fixation for development of communities of T. testudinum in Biscayne Bay, and nearby regions, is difficult to assess. The results from Soldier Key suggest that activities in the rhizosphere are more important than those in the phyllosphere. This aspect, however, requires further studies at more sites. N_2 fixed in the phyllosphere probably stimulates the growth of other epiphytes on the leaves; certainly organisms associated with N_2 fixing blue-green algae can acquire fixed N_2 (Jones and Stewart, 1969; Pohl and Drath, 1975). Clearly more work is needed on both host-epiphyte and epiphyte-epiphyte relationships in sea grass communities (Harlin, 1975). We have related our results on N_2 fixation, both in the phyllosphere and rhizosphere, solely to the nitrogen required for leaf production. At stands of T. testudinum near Barbados and near Bermuda, the underground production of rhizomes and leaves amounted to 59% and 24%, respectively, of the total production (Patriquin, 1973). Data on formation of underground tissue are not available for our study region, and could decrease the apparent quantitative significance of the inputs by N_2 fixation. On the other hand, our assumption that the nitrogen in dead leaves is lost to the communities is an oversimplification. Even apparently minor inputs of nitrogen, by fixation, might be significant in maintaining the stability of a community if there is an efficient recycling of nitrogen within the community. There is an impetus to determine N_2 fixation by the direct method (Burris, 1972; Stewart, 1967) due to recent problems associated with the C_2H_2 reduction technique (Balderston, Sherr and Payne, 1976; Brouzes and Knowles, 1971; deBont and Mulder, 1976; Flett, Rudd and Hamilton, 1975; Oremland and Taylor, 1975). The move towards the ^{15}N-methodology will undoubtedly also assist in resolving questions concerning recycling of nitrogen, and nitrogen transfer between nitrogen fixing organisms and the macrophyte and its epiphytes.

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MANAGEMENT OF THE COASTAL ZONE WITH SPECIAL REFERENCE TO MANGROVE SHORES

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Abstract

Ownership of mangrove wetlands is in a confused state in some regions of the Caribbean. Some regions consider mangrove forests a natural resource. Other regions have openly opted for their elimination as public policy.

With the advent of a coastal zone management awareness, some mangrove forests have gained notoriety because of conflicting interests. Developers and conservationists seldom agree as to the best possible use of a mangrove forest.

Recent cases of mangrove management conflict will be presented, along with a list of recommendations that could help make the most intelligent utilization of this coastal resource.

Resumen

Los derechos de propiedad sobre pantanos de manglar no están del todo claros en algunas regiones del Caribe. Algunos consideran los manglares patrimonio natural. Otros han optado abiertamente en favor de su eliminación como política pública.

Con el recién generado interés en el sabio manejo de la zona costera, algunos manglares han adquirido fama como objetos de intereses en conflicto. Proyectistas y conservacionistas rara vez se ponen de acuerdo en torno al mejor aprovechamiento posible de un manglar.

Se relatarán casos recientes de conflictos en torno al manejo de manglares, junto con una serie de recomendaciones que podría ayudar a hacer el más inteligente aprovechamiento de este recurso natural.

1. INTRODUCTION

The term "mangrove" can be meant to apply to either a single tree or to a whole forest where one, several, or all the species of mangrove trees known to exist within the given biogeographic province may occur. Descriptions of mangroves date back to 305 B.C. The word "mangrove" itself probably has its origin in the Malay "mangin" the name given to those trees that grew along the shores and "bore roots" above like stems. The Spanish "mangle" is applied indiscriminately to all our mangrove species, but it is only the red mangrove, Rhizophora mangle, which "bears roots above like stems". These can come from either the stem (prop roots) or the branches (drop roots) which, in Puerto Rico, are described as "lágrimas de mangle" (mangrove tears).

It is said that 75 percent of the world's coastline between latitudes 25°N and 25°S is dominated by mangroves. Mangroves are a circumtropical phenomenon. In species composition, mangroves are classed as of the New World or the Old World. New World mangroves are those of the western coast of Africa and both coasts of tropical America. Old World mangroves are those of the Indo-Pacific region and the eastern coast of Africa, the Cape of Good Hope being the distributional boundary of African mangroves.

Mangroves are plants that thrive in salt or brackish water. Although originally land plants, they have evolved physiological tolerances to saline environments; but this, by no means, restricts them to saline conditions. Mangroves are facultative halophytes; they can withstand salt, but are not obliged to exist only where salt is present. In fact, all mangroves have been grown in a salt-free environment. Red mangrove grows best in fresh water; there are both landlocked mangroves and dry mangroves, though the latter are rare.

The success of mangroves along the coastal zone therefore is not so much because they need salt, but rather because they can grow where no other plants can compete.

2. MANGROVES OF PUERTO RICO

Mangroves of Puerto Rico which, for the purposes of this paper, are being taken as representative of those of the Caribbean, were first studied carefully by botanists who surveyed the flora of Puerto Rico and the Virgin Islands early in the century. The works of N.L. Britton and M.T. Cook stand out amongst the pioneers. Interest in the mangroves on the island then shifted toward their forestry. Holdridge (1940) discussed the possibility of managing the then-existing 16 000 acres of mangrove for exploitation, rotation and afforestation. Mangroves were the most important cash crop in 1940. Then, mangrove areas were leased for reclamation to pasture, coconut farming, or private use, at a rate of U.S.$ 2-5/acre/year. Holdridge designates mangrove reclamation around San Juan as the most noticeable. The dredging of San Juan Harbor provided the silt which was dumped over large expanses of mangrove. This, plus the dumping of garbage, eliminated many mangrove acres, later reclaimed as building sites. He also blames cane growers for the loss of mangrove areas stating, "Reduction of mangrove area can be attributed almost entirely to the influence of man and especially to the sugar cane growers. For example, the large Loíza Sugar Company has installed a system of large drainage ditches and power pumps in the San Juan District which allows them to cultivate cane on hundreds of acres of formerly marshy land."

Silvicultural interest in mangroves in Puerto Rico has persisted. F.H. Wadsworth (1959) indicates a historical loss of some 12 000 acres from the original 30 000 acres presumed to have been supported by the Puerto Rican coasts, and states, "The decrease in mangrove area, while substantial, is less remarkable than the fact that this forest has resisted encroachment so well. Accessible to the earliest coastal settlements along harbours and protected estuaries, the entire mangrove has been cut over, most of it many times. Decades of the extraction of charcoal-wood resulted in repeated clear-cutting of stands as soon as the trees reached two or three inches in diameter. Much of the mangrove that remains is immediately adjacent to highly developed urban or agricultural lands. Locally no other type of forest has survived such heavy and repeated cutting nor such close proximity to the densely populated areas."

More recently the interest of marine biologists and general ecologists has been added to the interest of botanists and silviculturists in the mangroves of Puerto Rico. Golley, Odum and Wilson (1962) calculated the gross metabolism of a Parguera mangrove. Almodóvar surveyed the marine algae of Guánica Harbor (1964a) and of Jobos Bay (1964b). Glynn (1964), in his description of the invertebrate fauna of the shallow waters of Puerto Rico, discussed the common components of marine mangrove communities at La Parguera. Pagán and Austin (1970) reported on a massive kill in a mangrove embayment, Laguna Joyuda, in 1967. Matthews (1967), in her general description of coastal marine communities, also described and illustrated carefully a typical marine mangrove assemblage. Cintrón (1970) studied a mangrove-lined luminescent bay in Parguera. Austin (1971) surveyed the ichthyofauna of the mangroves of Western Puerto Rico, and Austin and Austin (1971) reported on the feeding habits of the juvenile marine fishes which spend their early life in the mangroves of western Puerto Rico; their study included 28 species. Almodóvar and Pagán (1971) described the flora and fish fauna of a mangrove lagoon and mangrove channels at La Parguera.

More recently, since the advent of P.R. Law No. 9 of 18 June 1970, which requires an environmental impact statement to be filed with all applications for permission to carry out development projects in Puerto Rico, a number of studies have been carried out in the island's mangrove systems. Many of these have been undertaken by government scientists in order to gather data that might be useful to forestall a project under consideration.

3. SHORELINE MANGROVES

The mangrove channels and embayments along the shoreline at places such as La Parguera, P.R., can be considered negative estuaries. This means that, since no rivers or streams drain near the area, the salinity along the shore may be higher than that of normal sea water (35 parts per thousand) because of evaporative concentration.

The mangrove channel bottoms are covered with the marine flowering plant *Thalassia testudinum*, the blades of which might, in turn, be covered with algae such as *Dyctyota divaricata*, *Laurencia obtusa*, *Polysiphonia*, *Caulerpa verticillata* and *Acanthophora spicifera* (Almodóvar and Pagán, 1971). *Udotea flabellum*, *Penicillus capitatus* and *Avrainvillea longicaulis* are other algae found commonly over the bottom in the mangrove channels, independent of the *Thalassia* blades.

The medusa *Cassiopea frondosa* is commonly found in the channels. Not so common is *Cassiopea xamachana*. Another invertebrate often seen in the channels is the large starfish *Oreaster reticulatus*. The giant sea cucumber, *Ludwigothuria mexicana*, is ubiquitous. It is constantly passing bottom sediments through its gut and a cluster of fecal pellets, consisting of little other than sand, silt and mud is almost invariably seen at its rear end. Pen shells, *Pinna* and *Atrina*, are often found here by summer students, as are the young of the queen conch, *Strombus gigas*, and an occasional tulip shell, *Fasciolaria tulipa*.

Although the waters in these channels are normally quite clear, a careless kick with a flipper, or a boat propeller passing over the shallows, will invariably create a cloud of mud and fine sediments which prevents any further underwater observations that day. In the larger embayments the waters are not so clear. Wind and jarea or mullet (*Mugil* spp.) keep the bottom stirred sufficiently to make the waters turbid in some bays. In others, plankton blooms of organisms, such as the luminescent dinoflagellate *Pyrodinium bahamense*, can be dense enough to restrict visibility.

The red mangrove, *Rhizophora mangle*, typically borders the channels and mangrove shores of Parguera. Their drop roots and prop roots, underwater, provide sessile marine organisms with the only hard substrate available within the channels. These roots soon become so densely covered with animal and plant growth that the stems bearing them often bend under their weight. This causes the trees to tilt, or even fall, toward the channel, giving rise to the illusion that mangrove trees "walk toward the water".

Sponges such as *Tedania ignis*, *Callyspongia*, *Ircinia*, *Chondrilla*, *Haliclona*, *Pellina*, and many others, are often found covering the roots. Hydroids such as *Myrionema amboinense* are frequent, as are other hydroids that grow in smaller and less conspicuous colonies. Sea anemones of the genera *Aiptisia* and *Bartholomea* are common inhabitants. *Sabellastarte magnifica* is the most common large polychaete. A smaller worm, equally abundant, is *Sabella melanostigma*. *Isognomon alatus* is the most common oyster on the roots, but *Crassostrea rhizophorae*, *Pteria* and *Brachydontes* are also present. Among the crabs, *Microphrys bicornutus* is often collected, although the most common crab among the roots out of water is the bright red and black *Goniopsis cruentata*. Up in the drop roots, branches and stems, another crab, *Aratus pisonii*, is very abundant. A snail, *Littorina angulifera*, shares this arboreal domain.

The predominant mangrove tree in Parguera is the red mangrove. These not only border the channels, but also form islets cresting the reef flats of offshore reefs. Its wood is used for fish traps, posts and pilings. "Elbows" are sought by boat builders, who painstakingly seek out the right bend and the right bole. Wadsworth (1959) reported that 10 million mangrove posts were consumed yearly in Puerto Rico. The bayonet-like red mangrove seedling, "tabaco de mangle", is often used by the fishermen who claim that these, stuck into their mouths, quench their thirst.

In the centre, or behind the more mature red mangrove stands, *Avicennia germinans*, the black mangrove, is quite abundant. The roots of these trees have a special adaptation for survival in the reducing environment of the soil. Vertical projections, or pneumatophores, stick out of the mud and offer a substrate upon which the snail *Melampus coffeus* is often found. Also among the pneumatophores thrive the burrowing fiddler crab, *Uca*, and the snails *Batillaria minima* and *Neritina virginea*.

The white mangrove, *Laguncularia racemosa*, can be found behind the black mangrove or mixed with it. *Laguncularia* has neither prop roots nor pneumatophores; its diagnostic field character is the presence of two glands at the base of each leaf. Further up, on dry land, one sometimes finds the buttonwood or Mangle Bobo, *Conocarpus erectus*. This is the rarest of all mangrove trees, not just in La Parguera, but throughout Puerto Rico.

Other plant species of the mangrove association are the salt grasses *Batis maritima* and *Sesuvium portulacastrum*, and the frescura tree, *Thespesia populnea*. *Hibiscus* can be seen at the edge of some mangroves in the Caribbean.

4. INSHORE MANGROVES

Puerto Rico's largest inshore mangrove is the Torrecilla-Piñones-Vacía Talega forest. If the dominant ecological feature of the Parguera mangroves is the ocean, then the dominant feature of this inland forest is the water table (ground water) and the Loíza River. According to Davis (1940), the water level above or below the soil, and with or without the direct intervention of the tide, probably has more effect upon plant zonation in the mangrove swamps than any other factor. The Torrecilla-Piñones-Vacía Talega mangrove lies squarely within the flood plain of the Loíza River.

Water within this inland mangrove, Vacía Talega for short, ranges between brackish and fresh. It has a small connexion only with the Atlantic Ocean, via the Boca de Cangrejos Inlet. Water flow and tidal fluctuations within the forest are negligible or non-existent (Hernández Avila *et al.*, 1974). Under such conditions it is not surprising then that marine organisms are absent. Only in one of the western canals of the inner lagoon, Laguna Piñones, was there evidence of salt water intrusions, indicated by a barnacle (*Balanus*) and an anemone (*Aiptisia*). The terrestrial mangrove crab, *Goniopsis cruentata*, was seen here, as was also the tree crab, *Aratus pisonii*. The snail *Melampus coffeus* can be found among the pneumatophores of *Avicennia* and the fiddler crab, *Uca*, is present both here and along the banks of the Loíza River.

As would be expected in reduced salinities, development of red mangrove here is outstanding. Straight-boled red mangrove trees, 50 ft or taller as seen here, are rare or absent from mangrove stands along the shore. Within the flooded portions of this forest, where the water is waist deep or deeper, red mangrove is dominant. In the shallower portions black mangrove dominates; the profusion of pneumatophores here is remarkable. White mangrove is mixed and abundant, and is the dominant tree along the man-made flood control canals and on the fringes of clearings. Mangle Bobo, Conocarpus, can be seen in the dry portions, but is never abundant and never in pure stands.

Two species of the large fern Achrostichum, A. aureum and A. danae, are found here. The "marunguey", A. aureum, is a conspicuous component of this assemblage. This fern is capable of living in fairly wet areas and its propagation is restrained by canopy cover. According to Holdridge, this fern can be kept under control provided the canopy cover is complete, but, if there is any clearing, either because of man or wind clipping, the marunguey will thrive in the sunlight and take over in such a way that future repopulation by mangrove becomes unlikely. Some students of mangrove ecology consider this fern a pest if unchecked. Holdridge (1940) recommends clearing A. aureum by fire if it is to be kept at bay.

Regarding the fish fauna of the Vacía Talega mangrove, the only fish found here are those which have been introduced. The mosquito fish, Gambusia affinis, was introduced in 1914, and the guppy, Lebistes reticulatus, in 1935. The "Guavina", Gobiomorus dormitor, has been reported. Within the channels near the lagoons there is another introduced fish, the Java tilapia, Tilapia mossambica, introduced as recently as 1958. This mangrove had no ichthyofauna until fish were introduced there by man.

5. LANDLOCKED MANGROVES

Along the north coast of Puerto Rico there are mangrove patches completely isolated from coastal or river waters, such as the one at Carrizales. This, a patch of mangrove behind the coastal dune, had a moat around it until a part was filled for reclamation. The water in this moat could fluctuate between hypersaline and fresh, depending upon rain water or spillage of heavy seas over the dune.

At Mona Island, 50 mi west of Puerto Rico, there is a mangrove stand not only landlocked and several hundred metres from the shore, but also dry except during extremely heavy, and infrequent, rains. Red mangrove is the predominant form, with white mangrove also present.

6. MAN-MADE MANGROVES

There are places in the world where mangroves have been planted by man; Hawaii offers an interesting case. Prior to 1902 there were no mangroves in Hawaii. At that date Rhizophora mangle, of the "New World", was introduced. In 1922 the Indo-Pacific, or "Old World", species R. mucronata was introduced, but it did not have the success of R. mangle in invading the sheltered coves and bays where Hibiscus might once have been dominant. A description of this planted swamp is found in Walsh (1967).

7. RESISTANCE

Mangroves are anything but delicate plant species. We have seen mangroves thrive at the outfall of sewage treatment plants, in hot water, survive oil spills and resist man's encroachment. We have mangrove patches growing surrounded completely by fill, construction, or roads. An area of mangrove, cleared and dyked for a roadbed, now has mangroves growing on both sides of the dyke, regardless of distance from the culverts. Since mangroves are so hardy, their management does not present serious problems.

Mangroves do die, however. They will be killed by frost, by drastic changes in water level, by floods where waters are retained for long periods and by fill. Mangroves are very susceptible to wind damage during storms and to heavy surf; but the recent preoccupation regarding the delicate balances that dictate mangrove survival is mostly unwarranted.

8. MANAGEMENT ISSUES

Large expanses of mangroves in Puerto Rico are in private hands. Before the 20th century mangrove lands were ceded by the Spanish Crown as a reward to loyal island residents. After the Spanish-American War the new Government chose to honour the Crown mangrove concessions by decree.

A Reclamation of Arid Lands and Swamp Lands law was passed in 1948. The preamble of this law reads:

> "It being the case that the amount of agricultural lands in Puerto Rico is limited and not sufficient to sustain its dense population, it becomes necessary and urgent to take maximum advantage of the available agricultural resources, gathering from them the greatest possible return within the reasonable norms of cost and effort, and offering greater opportunities for employment. The existence in Puerto Rico of some 16 000 cuerdas of wastelands in the form of wet swamps or mangroves which could stand reclamation, improvements, or conversion into fertile and highly productive land is, therefore, not justifiable. Such wastelands are, in addition, sources of infection and nurseries for malaria-transmitting mosquitoes and must, therefore, be eliminated." (Author's translation)

Funds were appropriated under this law to assist the private owner in the reclamation of his mangroves. Reclaimed mangroves were tax-exempt for ten years if they were destined for work camps or farming. Those mangrove areas designated by the Government as unhealthy were to be reclaimed by their private owners or they would be expropriated, with subsequent reclamation by the Government itself. This law was revised in 1959 in order to define more clearly the ultimate fate of the monies destined toward reclamation. It is not surprising therefore that, in Puerto Rico, there is a lack of respect toward mangroves as a natural resource.

Mangroves have suffered cutting and clearing for the establishment of boat-houses. This has happened extensively in one area along our south-west coast and is now progressing into another. No corrective measures have been taken and there are expressions, attributed to the highest concerned official, to the effect that nothing will be done. Mangroves make excellent garbage dumps. Several municipalities dispose of their garbage in mangrove areas, two of which happen to be bird sanctuaries and natural preserves. Refineries and other petrochemical facilities have been placed in mangrove areas. Even construction of a thermonuclear generating complex was slated for a mangrove area: our largest marine mangrove ecosystem. Construction was stopped some U.S.$ 30 million later, ostensibly on account of a geologic fault. The site did not go to waste however; two fossil-fuel generating complexes are today producing power there. Their construction eliminated some 200 acres of mangrove and their operation and subsequent development threatens 1 100 more. As an excellent example of the vagaries of political ecology, the same individual who, as an employee of the power company, was charged with getting the project to completion, mangrove destruction and all, later became executive director of the Government agency charged with enforcing the absolute preservation of every mangrove plant in Puerto Rico.

The official attitude toward mangroves and other coastal resources has gone from total contempt (Law of 1948), through the sublime (Law 9 of 1970) and into the ridiculous (Ruling on Mangrove Preservation of October 1974). This evolution itself is worthy of mention. A conservational awareness developed in Puerto Rico in the early 1960s. Insular legislation was enacted to protect our beauty spots and natural resources. Perhaps our most famous coastal beauty spot, natural resource and tourist attraction is a bioluminescent bay at Parguera. The P.R. Planning Board commissioned a study relative to coastal bays. The study revealed that the luminescent bay had a fringe of mangrove, as does most of the south-west coast. On the basis of this observation it was concluded that, in order to preserve the ecological integrity of embayments along the north coast, a comparable fringe of mangrove was necessary. The study recommended that a mangrove strip 700 to 1 000 ft wide be maintained along lagoon shores to protect their ecology (Candelas et al., 1968). The Board adopted this strip as a ruling and, in its Land Use Plan for Metropolitan San Juan, it keeps a mangrove buffer between areas designated for development and the mangrove lagoons.

Bioluminescent lagoons then became sacrosanct. All that was needed to justify the protection of any area was to say that it was near a luminescent lagoon. Not known at that time were the facts that the bioluminescent bay was both a relatively recent phenomenon, absent from charts and maps before the 1870s (Cintrón, 1970), and was susceptible to periodic pollution. A salina behind the bay, in operation since 1937, occasionally dumps its brines into the bay. This makes the bottom waters anoxic and hypersaline, raising the salt content up to 57.3 parts per thousand (Cintrón et al., 1970). The brine pollution apparently had little or no effect upon the surface and its luminous displays.

Recent rulings and present public policy have all but done away with the original well-meant intent of sound ecology. A ruling meant to protect coral reefs now purports to protect all coral colonies. If it were obeyed or enforced to the letter, there would be legal grounds to halt the maintenance dredging of San Juan Harbor should a piece of coral come up in the dredge spoils. The policy meant to protect mangrove forests now protects all mangrove plants, even if these are stray scrubs of no ecological value.

Fishermen have been served a summons for cutting mangrove poles to make fish traps. Fish traps have been made of mangrove wood for generations; now it is a crime. The existence of a mangrove shrub gives preservationist pressure groups legal grounds to halt the rechannelization of a canal that is nothing but an open sewer. Even the Model Cities Program could be impaired on account of the mangrove which has repopulated the area after the slum was cleared some twenty years ago. This mismanagement of conservation policy only reflects upon the ecological ignorance of the enforcer.

We must reconsider our whole conservation and resource management policies in order to ascertain whether or not the original intent of the policy still exists in its application. I am convinced that in some cases environmental rules have been wielded as useful weapons for private or political advantage. This is most insiduous when each project or activity is viewed on a case-by-case basis. In other cases, the rules have been enforced to the letter, when their enforcement made little or no ecological sense.

9. RECOMMENDATIONS

Any recommendation made toward coastal resource management, or any resource management, must contain an inherent flaw in policy. Policy presupposes legality. Legality presupposes equality. Equality is not a natural phenomenon. Not all resources are equally important from an ecological standpoint. It could be that the most magnificent ecological resource to some, is of no value to others. The Caribbean is a daily witness to visitors who tell us about the magnificence of resources which we would gladly exchange for other values. Ecological resources are designated as such by ecologists. Not all ecologists are holy, and none has all the answers. When an ecologist views a resource he can make three mistakes:

(1) he believes what he is seeing is true;

(2) he believes that is how it has always been;

(3) he believes that is how it must forever be.

All wise management, and all wise policy, must take these limitations into account.

9.1 Inventory

The first step toward sound management is knowing what it is that must be managed. Governments must inventory their resources and then take a hard look to ascertain what these are worth to them. Expertise should be sought wherever available but, in the final analysis, cultures do think differently. Decisions will have to be made as to where the authority lies for management: owner or neighbour.

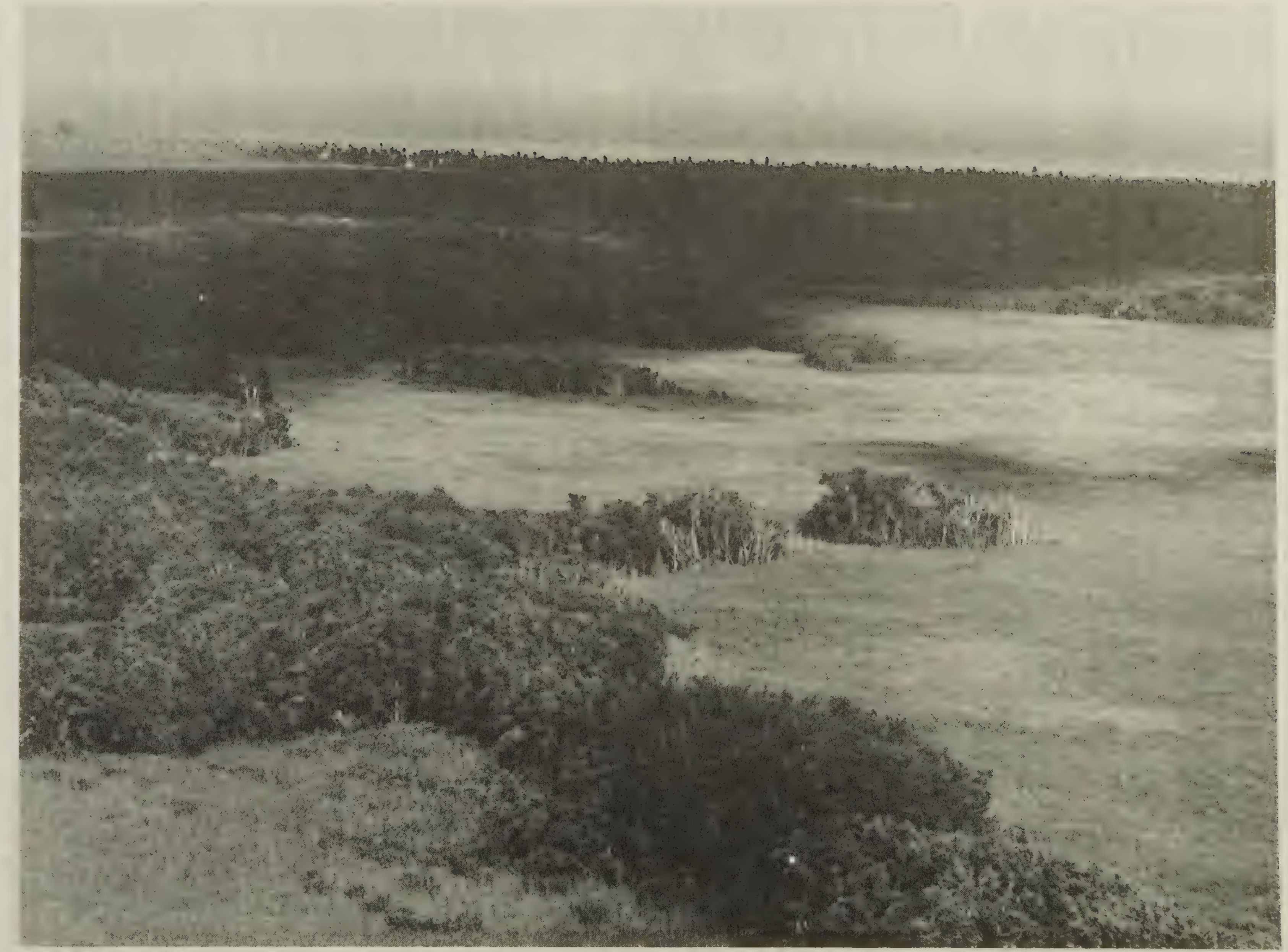

Fig. 1 Mangroves were the most important cash crop in 1940. They were exploited for charcoal and were leased for reclamation and pasture at a rate of U.S.$ 2–5/acre/year. There are reports that 10 million mangrove posts were consumed yearly in Puerto Rico

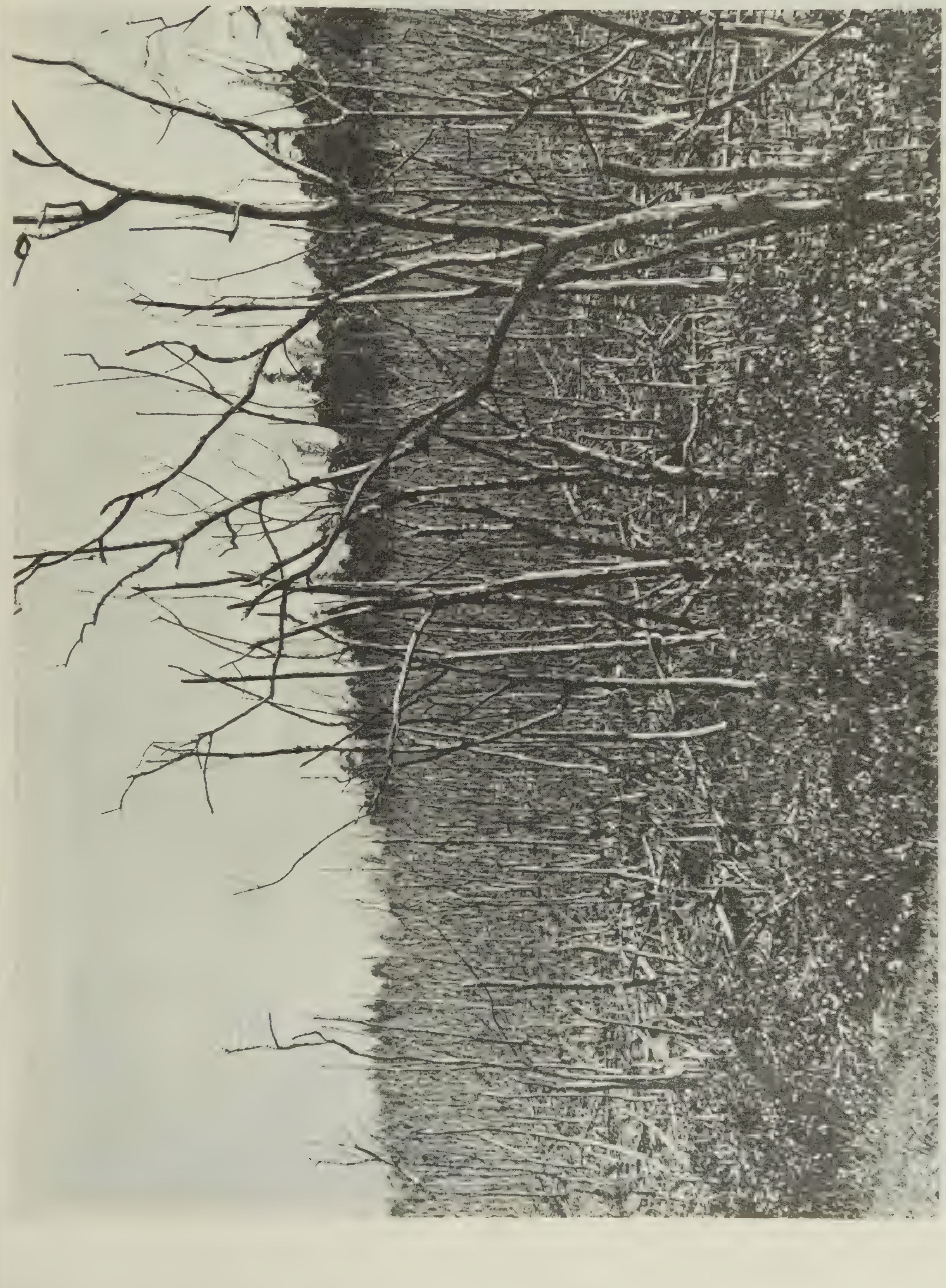

Fig. 2 A mangrove stand whose death resulted probably from earth movements and sand extraction during the construction of the International Airport at Isla Verde

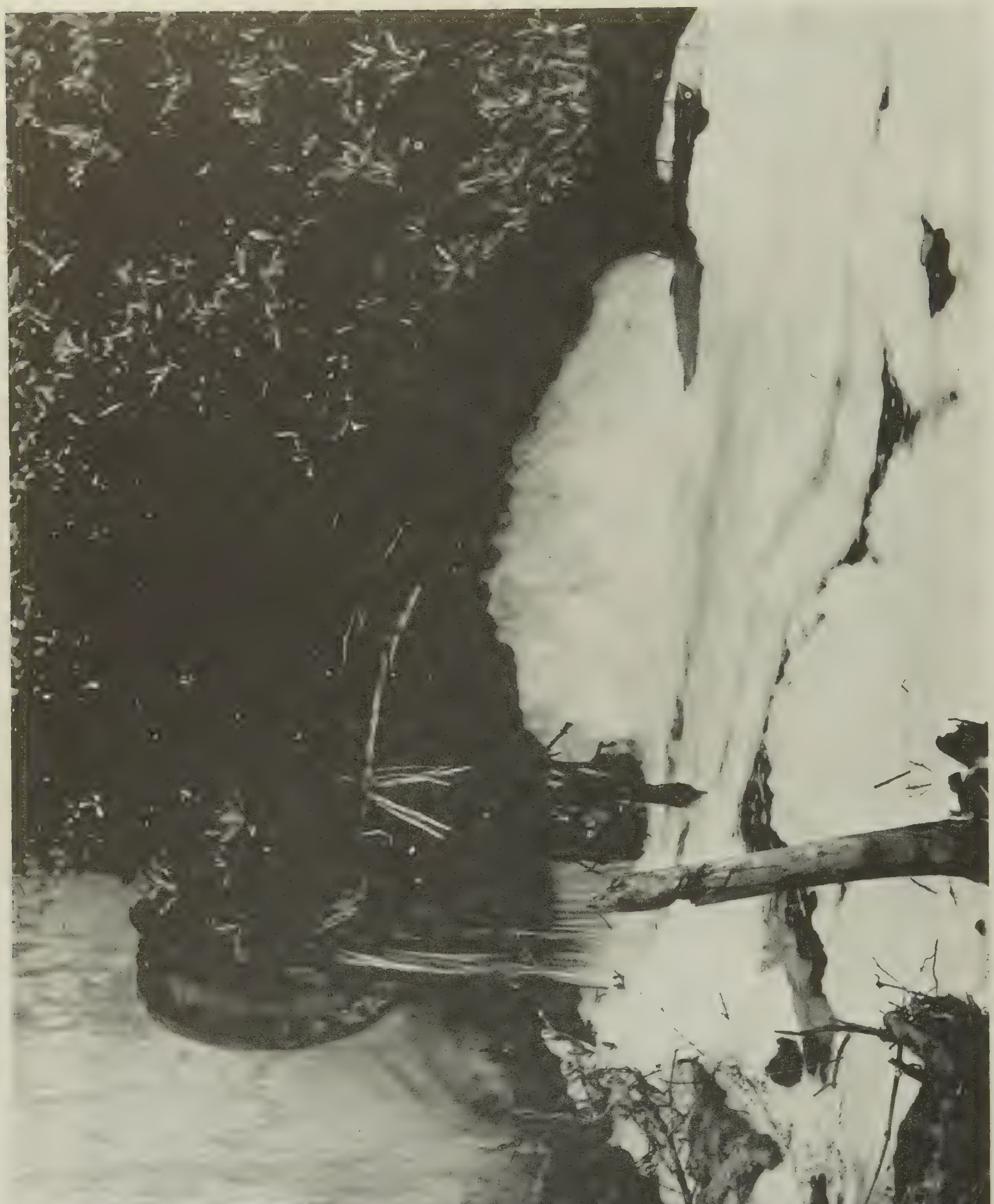

Fig. 3 Mangroves are anything but a delicate plant species. Some may survive a fairly high degree of pollution and may actually live at the outfall site for domestic sewage

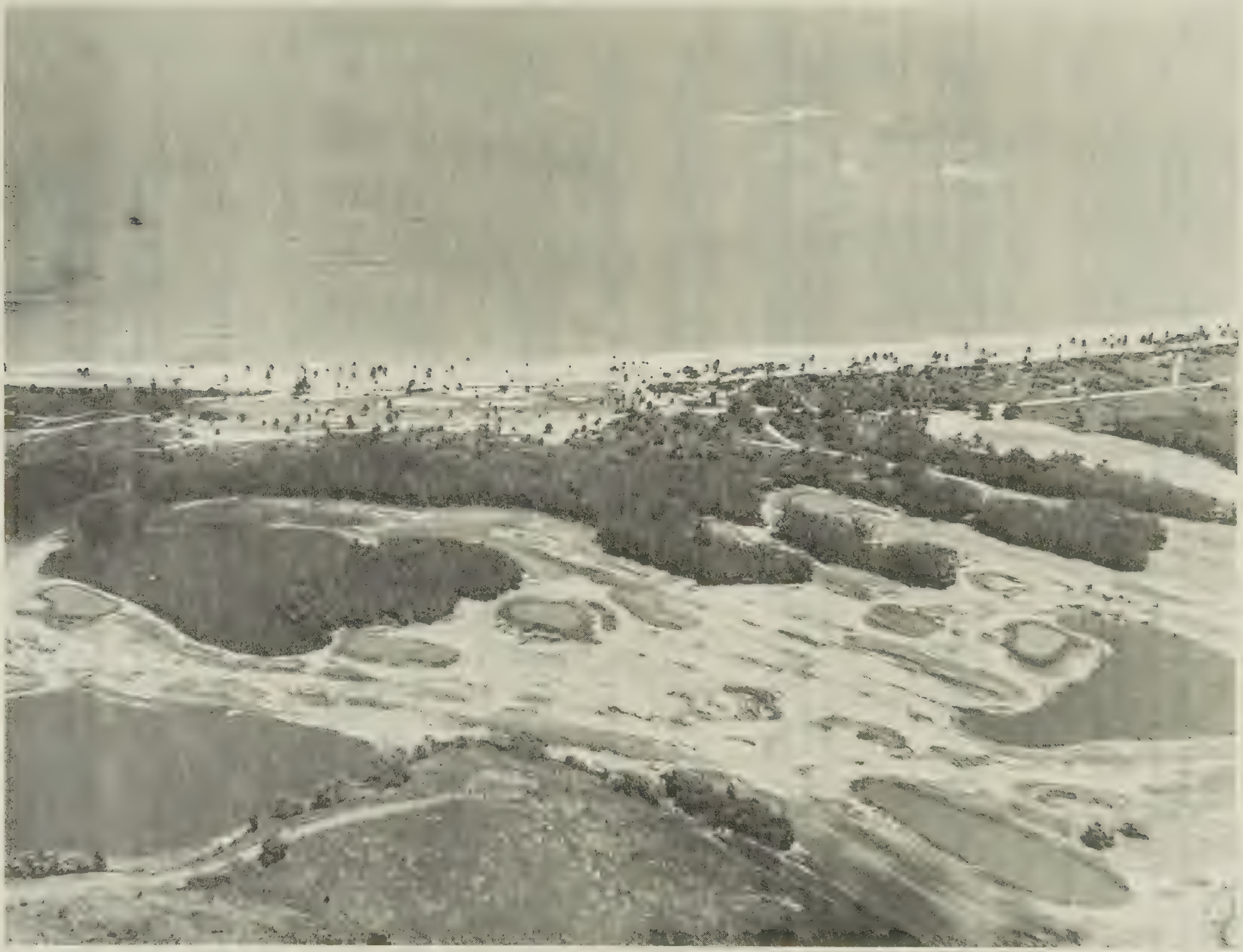

Fig. 4 Mangroves may be used successfully as an element in landscape architecture. They have been planted in private gardens and have been used in golf courses

9.2 Evaluation

Each resource must be evaluated. Not all reefs are alike, and not all reefs are equally important. Countries must then designate three sets of resources:

(1) those which should be preserved at all costs;

(2) those the fate of which is negotiable, depending upon what is to be gained by their utilization;

(3) those which are expendable.

9.3 Planning

A colleague of mine says Columbus was the first planner because, when he sailed, he did not know where he was going, when he got there he did not know where he was and the Government footed the bill (Villamil, personal communication). Once a resource evaluation and designation has been carried out, then master plans must be enacted and obeyed.

9.4 Support

Setting aside an area as a resource does not guarantee its conservation. Unless funds are set aside to guard, manage, protect and maintain the sanctuaries, these will continue to be abused. Setting aside an area for conservation should be an active and not a passive commitment.

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ASPECTS OF PHYTOPLANKTON DYNAMICS IN THE CARIBBEAN SEA AND ADJACENT REGIONS

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Abstract

Phytoplankton dynamics are intimately related to patterns of oceanic and atmospheric circulation. Major features of circulation in the Caribbean Sea include the characteristic northwestward flow of surface waters, the large cyclonic gyre over the Colombia Basin and the cross-current convection régime maintained by the prevailing tradewinds. Upwelling occurs along the southern margin and sinking along the northern margin. Offshore waters are well stratified.

Nitrogen limitation appears to be crucial to phytoplankton productivity. Significant nitrogen enrichment occurs in areas of upwelling. Enrichment by continental runoff is dependent upon the geology of the drainage basin. Mixing across the pycnocline induced by the proximity to land masses accounts, in part, for the fertility of near-shore areas. Oscillatoria is unique among the phytoplankton in its ability to fix molecular nitrogen and its large standing crops in permanently stratified waters. A number of mechanisms act in excluding this organism from areas of upwelling.

A powerful tool in the study of phytoplankton dynamics is provided by satellite imagery. Large concentrations of phytoplankton may be directly visualized. Changes in distribution patterns can be monitored using successive satellite overpasses. Large plumes and ocean fronts are readily apparent as shown by imagery of the upwelling along the Guajira Peninsula.

Resumen

La dinámica del fitoplancton está intimamente ligada a los patrones de circulación marina y atmosférica. Dentro de las características notables de la circulación del Mar Caribe se incluye la deriva de aguas superficiales en dirección noroeste, el giro ciclónico

sobre el extremo occidental del área colombiana y el régimen de convección que resulta en surgencia a lo largo del margen meridional y hundimiento de aguas superficiales a lo largo del margen septentrional. En general, las aguas alejadas de la costa presentan una estratificación notable.

La productividad del fitoplancton en aguas tropicales parece estar estrechamente controlada por la tasa de suministro de nitrógeno fijado a la zona eufótica. Las áreas de surgencia representan focos de enriquecimiento de nitrógeno. El enriquecimiento por aguas continentales depende de las características geológicas de la cuenca hidrográfica. La cercanía de masas de tierra induce procesos de mezcla a travez de la picnoclina lo cual aumenta la fertilidad de aguas costeras. La Cyanofita planctónica Oscillatoria se destaca por su capacidad de fijar nitrógeno molecular y por presentarse en grandes concentraciones en aguas tropicales estratificadas. Varios mecanismos contribuyen a excluir este organismo de las áreas de surgencia.

La tecnología espacial ofrece una poderosa herramienta en el estudio de la dinamica del fitoplancton. Algunos sensores pueden producir imágenes que documentan la distribución superficial del fitoplancton. Los cambios en distribución pueden ser estudiados por medio de pases sucesivos del satelite. Los ejemplos presentados referentes al área de la Guajira ilustran la versatilidad de estos instrumentos en el estudio del fitoplancton.

1. INTRODUCTION

Those who are familiar with the work presented at the Symposium preparatory to CICAR will find that the subject matter of the present paper is closely related to that of a paper delivered by Margalef (1971) at the time. It is thus both a challenge and an honour to attempt to bring a fresh view of some aspects of phytoplankton dynamics in the Caribbean.

My original purpose was to discuss only my own work on the phytoplankton of the upwelling area off the Guajira Peninsula in the Colombian Caribbean. At the request of Dr. Wickstead, I have expanded my presentation to include other regions within the scope of CICAR and, at the same time, attempted to formulate some ideas as to how we should direct future research in the area.

2. THE PHYSICAL SETTING

At the risk of retracing a well-worn path, I would like to review some of the main aspects of oceanic and atmospheric circulation which profoundly affect phytoplankton dynamics in the Caribbean.

Studies of the Caribbean circulation have been carried out by Wüst (1964), using the core method; by Gordon (1967), using geostrophic analysis and by Fébres-Ortega (1972), using isanosteric analysis. These studies emphasize the characteristic northwestward flow of surface waters which is an extension of the large-scale circulation of the Atlantic Ocean. A prominent feature of this surface circulation is the appearance of a large cyclonic gyre over the southwestern corner of the Caribbean. This circulation pattern dictates the occurrence of a zone of convergence as the cyclonic current turns back upon the main axis of circulation.

Superimposed upon the horizontal circulation is a distinct convection régime typified by upwelling along the southern margin and sinking along the northern margin. Gordon (1967) attributes this pattern to Eckman drift induced by the prevailing tradewinds, which blow northeasterly for the greater part of the year. Major regions of upwelling are in the vicinity of Margarita Island, off the east coast of Venezuela, and off the Guajira Peninsula, in the Colombian Caribbean. Upwelling also occurs over the Campeche Banks and west of Florida in the Gulf of Mexico. Robinson's atlas of temperatures and thermocline depths (1973), gives a clear view of the seasonal fluctuations in distribution of the centres of upwelling and sinking. A large body of literature exists concerning the physics, chemistry and biology of the Venezuela upwelling, most of which has been listed by Margalef (1971). Comparatively few studies have been carried out in the Guajira upwelling. Redfield (1956) provided some data on the eastern end of the peninsula in his study of the hydrography of the Gulf of Venezuela. The Colombian Navy - ARC, DIMAR - has published technical reports of oceanographic cruises in the area. These data have been used by Fajardo (1975) in describing the horizontal and vertical distribution of water masses as affected by the upwelling process.

The tradewinds, in addition to their effect on water mass movement, greatly affect the climate along the southern coastline of the Caribbean. The area is characterized by an alternation of dry and wet climates. The semi-arid condition of the Guajira and Paraguana peninsulas is in striking contrast to the almost daily rainfall experienced in the Darien area at the base of the isthmus of Panama. Lahey (1973) interprets the aridity of coastlines aligned in east-west direction to be a consequence of increased frictional drag over the land surface as compared with the sea surface. The increased drag causes a southward diversion of flow which brings about subsidence of upper atmospheric layers over the coastal area. The result is a stabilization of the lower layers of the atmosphere and decreased rainfall. It is important to note that this weather pattern has a pronounced effect upon the marine environment by limiting continental runoff over long stretches of the coastline.

3. SUPPLY OF NUTRIENTS TO THE EUPHOTIC ZONE

It is well established that one of the major constraints to biological productivity in the oceans is the rate of supply of nutrient elements to the euphotic zone. Although phosphorus and silicon have been recognized as key limiting nutrients in the marine environment, Platt and Subba Rao (1973) pointed out the extensive experimental evidence which identifies nitrogen limitation as perhaps the single most important constraint to primary production in tropical seas. It is thus essential to identify and quantify the sources and sinks of nitrogen if one is to attain a measure of predictive capacity concerning fluctuations in biological productivity in these waters.

Upwelling appears to be the main source of nutrient input along the southern boundary of the Caribbean. However, the enrichment is relatively low when compared with better known upwelling ecosystems such as that off the coast of Peru. Maximum surface concentrations of NO_3-N recorded during our work in the Guajira area were between 2 to 3 µg-at $N \cdot l^{-1}$ under conditions of active upwelling. In contrast, Walsh and collaborators (1971) reported values of up to 30 µg at NO_3-N $\cdot\ l^{-1}$ for surface waters in the Peru upwelling. Low values for the Caribbean reflect the origin of the source water; the mass of the Subtropical Underwater. Defant (1961) identifies this mass as being derived from the homohaline top layer of the Subtropical North Atlantic. Regardless of these differences, phytoplankton response to enrichment by upwelling in the Caribbean is significant. Figure 1 documents the rapid disappearance of nitrate during a drogue study in the Guajira area. A parachute drogue was set at 10 m depth at a point of active upwelling and followed for two days, during which biological, physical and chemical parameters were monitored. Production, as estimated by the ^{14}C method, totaled 3.6 g $C \cdot m^{-2}$ over the 26-hour period throughout the euphotic zone (disregarding losses due to respiration). During this time a total of .5 g $N \cdot m^{-2}$ were consumed in the same water column.

The contribution of nutrient salts to the euphotic zone by way of continental runoff is variable and highly dependent upon the chemistry and geology of the drainage basin. Ryther et al. (1967) studied the effect of Amazon River runoff on the adjacent marine environment and found little evidence for enhancement of phytoplankton growth by nutrient enrichment. Riley's (1937) data show a significant increase in phytoplankton biomass in the region adjacent to the mouth of the Mississippi River; however, the river influence is only apparent within a 130 km radius from the river mouth. Recent work by Galiano (unpublished) on the Magdalena River indicates that large amounts of nitrogen, mainly in the form of dissolved ammonia and colloidal nitrogenous compounds, are discharged into the Caribbean. Calculations based upon his data yield mean discharge rates of 4.1 $kg \cdot sec^{-1}$. At present, no data are available regarding runoff in the southwestern corner of the Caribbean, an area of extremely high rainfall. One might expect that, due to the cyclonic gyre which occurs in the area, waters from the Magdalena and Atrato rivers would have an extended residence period in this region.

A mechanism of nutrient enrichment which has received recent attention is the "land mass effect". In addition to enrichment by runoff, inshore waters are locally enriched due to breaking of internal waves which brings about mixing of waters across the permanent pycnocline. Moreover, in shallow areas, nutrients from organic debris may be continuously recycled, rather than being lost to the abyssal regions, as occurs in deeper offshore waters. In the CICAR region, the studies of Sander and Steven (1975) off Barbados have provided valuable information concerning the response of phytoplankton to this type of enrichment.

Offshore regions of the Caribbean, and of tropical seas in general, are characterized by a marked thermal stratification which inhibits vertical mixing and is thus partially responsible for their relatively low fertility. Under these circumstances, the ability to exploit alternate nutrient sources becomes an important asset to planktonic organisms. In this respect, the capability of the planktonic blue-green alga Oscillatoria (Trichodesmium) to fix molecular nitrogen places it in a unique position among the phytoplankton. CarPenter

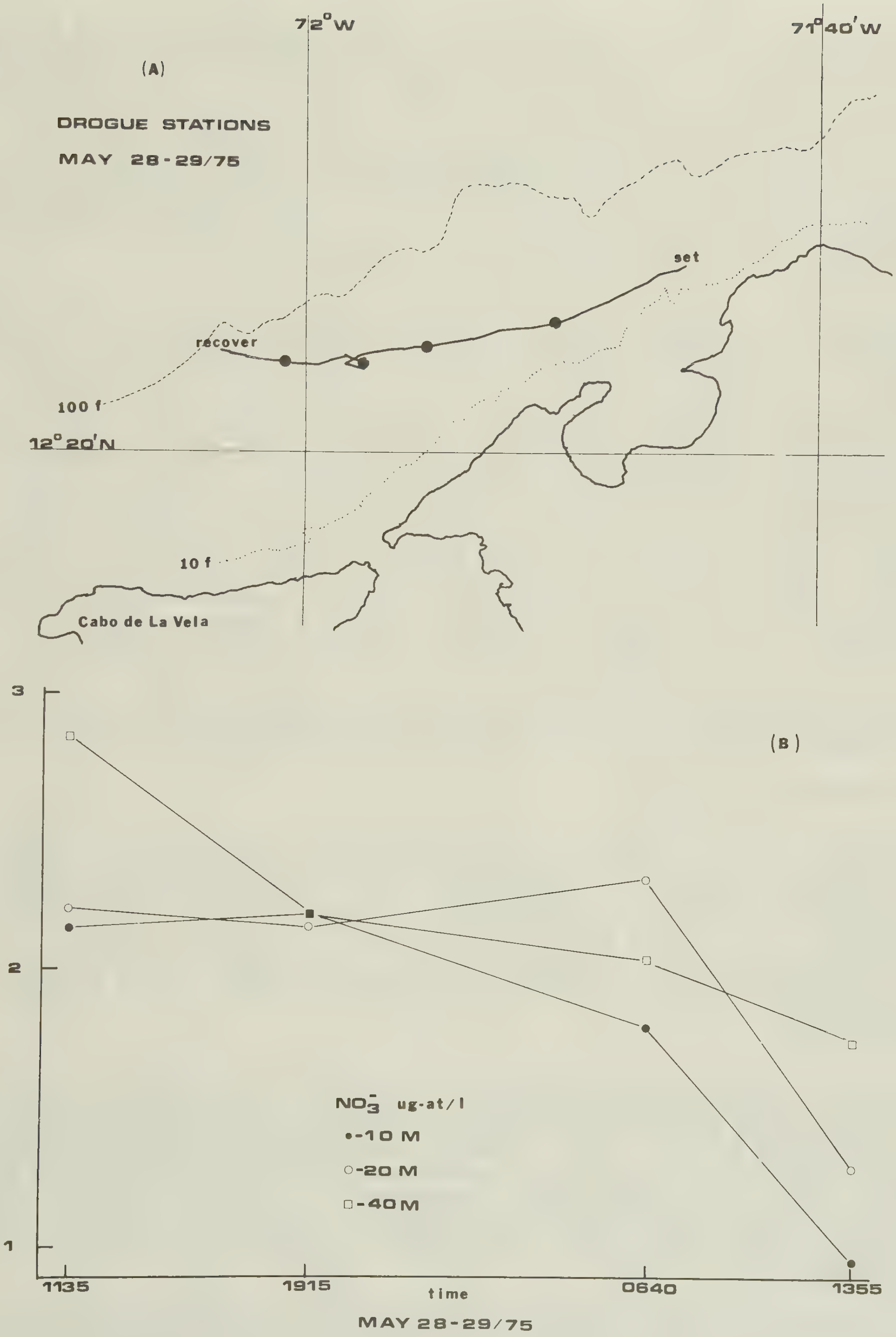

Fig. 1 Nitrate utilization during a drogue study in the Colombian Caribbean.
(a) Drogue track and location of sampling stations;
(b) Nitrate concentration at selected depths during the study

and McCarthy (1975) have provided an extensive bibliography concerning studies of nitrogen fixation by Oscillatoria. This organism is ubiquitous in stratified tropical waters, as is apparent from reference to the discussion of Taylor et al. (1973). In the CICAR area it has been reported by numerous workers: Margalef (1965), Acleto (1970), Bunt et al. (1970) Lopez and Vinogradova (1972), Sander and Steven (1973) and Carpenter and Price (1976). The literature stresses the dominance of Oscillatoria in terms of biomass with respect to other forms of phytoplankton over large areas of the tropical oceans. Carpenter (1975) states that this dominance is especially noticeable in the Caribbean Sea. It thus appears that Oscillatoria could well play an important role in the overall biological productivity of the Caribbean and other tropical seas. Unfortunately, little is known concerning the role of this cyanophyte in the trophic web of the pelagic environment.

Figures published by Margalef (1972) indicate that Oscillatoria is noticeably excluded from the Margarita upwelling in the Eastern Caribbean. A similar situation occurs in the Guajira upwelling as illustrated in Figure 2. Several factors contribute to this distribution pattern. As indicated by Carpenter and McCarthy (1975), maximum concentrations of Oscillatoria occur in the surface layers due to the buoyancy provided by an extensive system of gas vacuoles throughout the trichome. This distribution dictates a rapid "washout" under conditions of upwelling. These authors have also calculated half-saturation constants for the uptake of nitrogenous compounds by Oscillatoria. The values are well above those calculated for other members of the phytoplankton. Consequently, nutrient enrichment can be expected to bring about significant changes in the relative abundance of Oscillatoria. Finally, Carpenter (1976) has determined that nitrogen fixation by this organism is affected adversely by strong wave action, a prevalent condition in the Caribbean upwelling areas. The work of Capone in the Guajira upwelling (unpublished results) indicates that nitrogen fixation, as measured by the acetylene reduction technique, occurs only around the periphery of the upwelling area and only when Oscillatoria is present.

It is hoped that future research on this topic will be directed toward a quantitative evaluation of the contribution of reduced nitrogen by Oscillatoria and elucidation of the trophic relationship of this organism with other members of the pelagial.

4. REMOTE SENSING OF PHYTOPLANKTON

A recent development in the field of marine science is the increasing use of remote sensing techniques. Airborne applications require a substantial investment plus a detailed knowledge of instrument operation and maintenance. On the other hand, satellite imagery is becoming readily available in a pre-processed form as photographic reproductions or as computer compatible tape. Badgely et al. (1969) have edited an extensive review of the applications of satellite remote sensing technology to ocean science. A less technical account but, by the same token, an eminently readable one, has been published by Herrera (1969). Both these publications reveal biological information to be readily obtainable from satellite imagery.

The distribution of sea surface temperature is of interest to biologists of several disciplines. Thus, fishery scientists are aware that distribution of schooling fishes can be intimately related to sea surface temperature. Phytoplankton ecologists find that sea surface temperature data give a good indication of upwelling conditions which markedly affect production rates. At present, several satellites are equipped with infra-red radiometers capable of measuring this parameter. Perhaps the best of these, in terms of resolution, is the "very high resolution radiometer" (VHRR) of satellites NOAA 3 and 4. This instrument provides images of sea surface temperature distribution with a spot-size of a little under 2 kilometres.

LANDSAT I and II (previously ERTS) were designed mainly for monitoring land resources, but ocean applications have been numerous. These satellites are equipped with "multispectral scanners" (MSS), which independently scan bands of: 0.5–0.6, 0.6–0.7, 0.7–0.8 and 0.8–1.1 um. Data from these scanners are telemetered in digitized form to ground

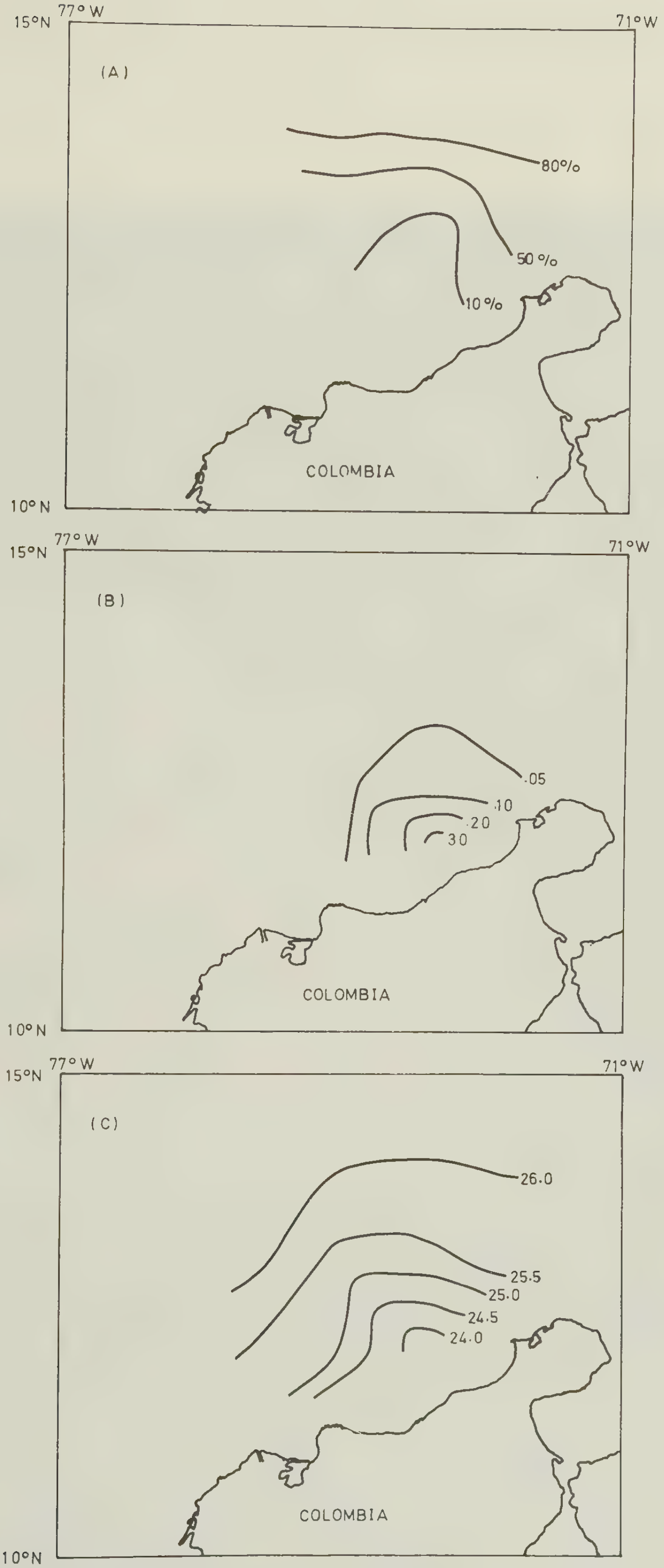
15°N
77° W
71°W
(A)
80%
50 %
10 %
COLOMBIA
10° N
15°N
77° W
71°W
(B)
.05
.10
.20
.30
COLOMBIA
10° N
15°N
77° W
71°W
(C)
26.0
25.5
25.0
24.5
24.0
COLOMBIA
10°N

Fig. 2 *Oscillatoria* distribution as influenced by the Guajira upwelling.
(a) Distribution of *Oscillatoria* as percent of net phytoplankton. Samples were taken from vertical hauls (0–50 m) of a 65 µm mesh net. *Oscillatoria* was counted as number of trichomes, all other phytoplankters as individual cells;
(b) Distribution of nitrate nitrogen concentration (µg at $\cdot$ l^{-1}) at 10 m depth;
(c) Surface temperature distribution (°C)

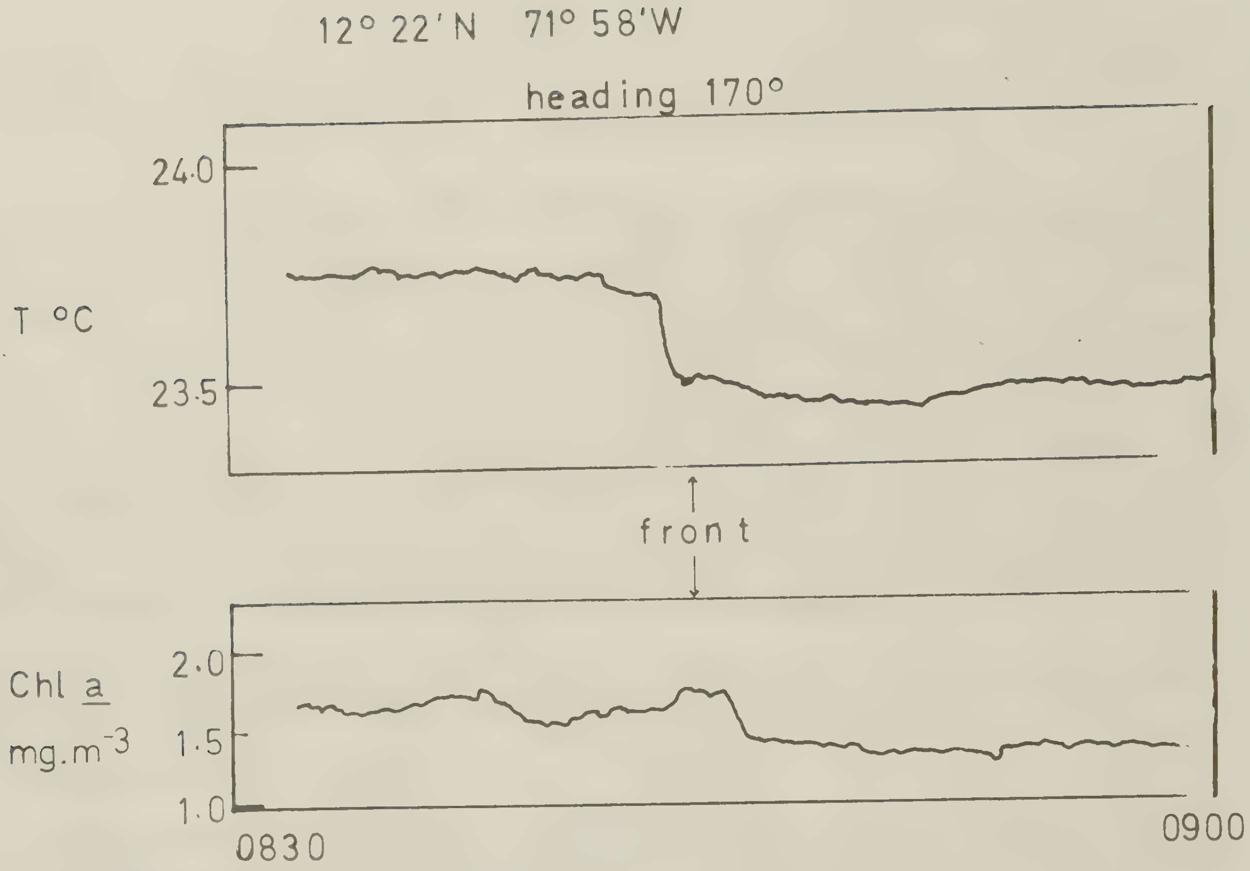

Fig. 3 Continuous traces of surface temperature and chlorophyll a concentration across a frontal zone. Underway sampling was carried out while steaming on course at 10 knots. A thermistor installed in the ship's sea chest was used to monitor surface temperature. Surface chlorophyll a concentration mg · m^{-3}) was followed using a flow-through recording fluorometer. Strip chart recordings were calibrated against replicates analysed spectrophotometrically following acetone extraction.

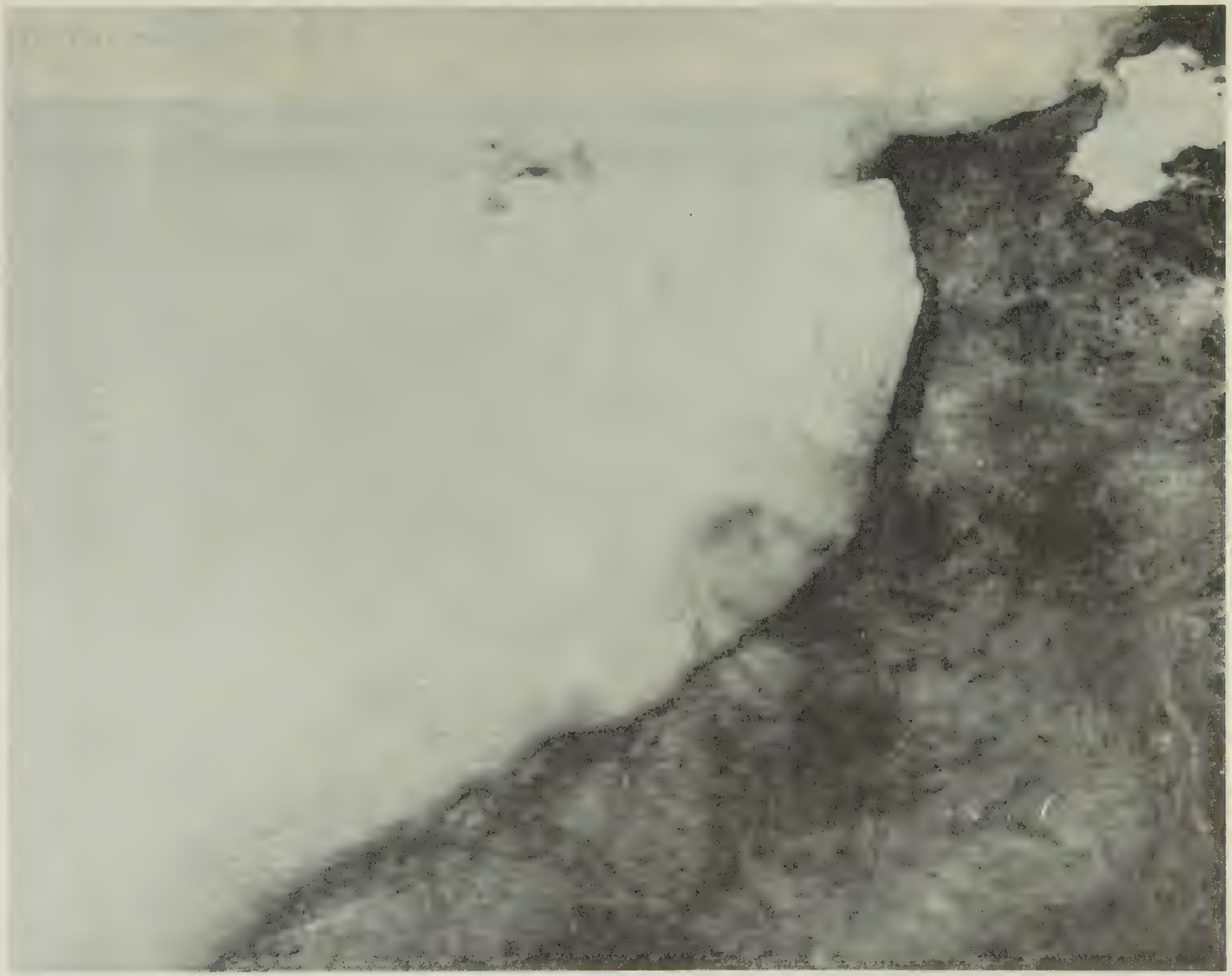

Fig. 4 a LANDSAT image of the Guajira coast (MSS 4 band) for 01 January 1973. Recently upwelled water is visable as a light grey plume extending southwest of Cabo de la Vela

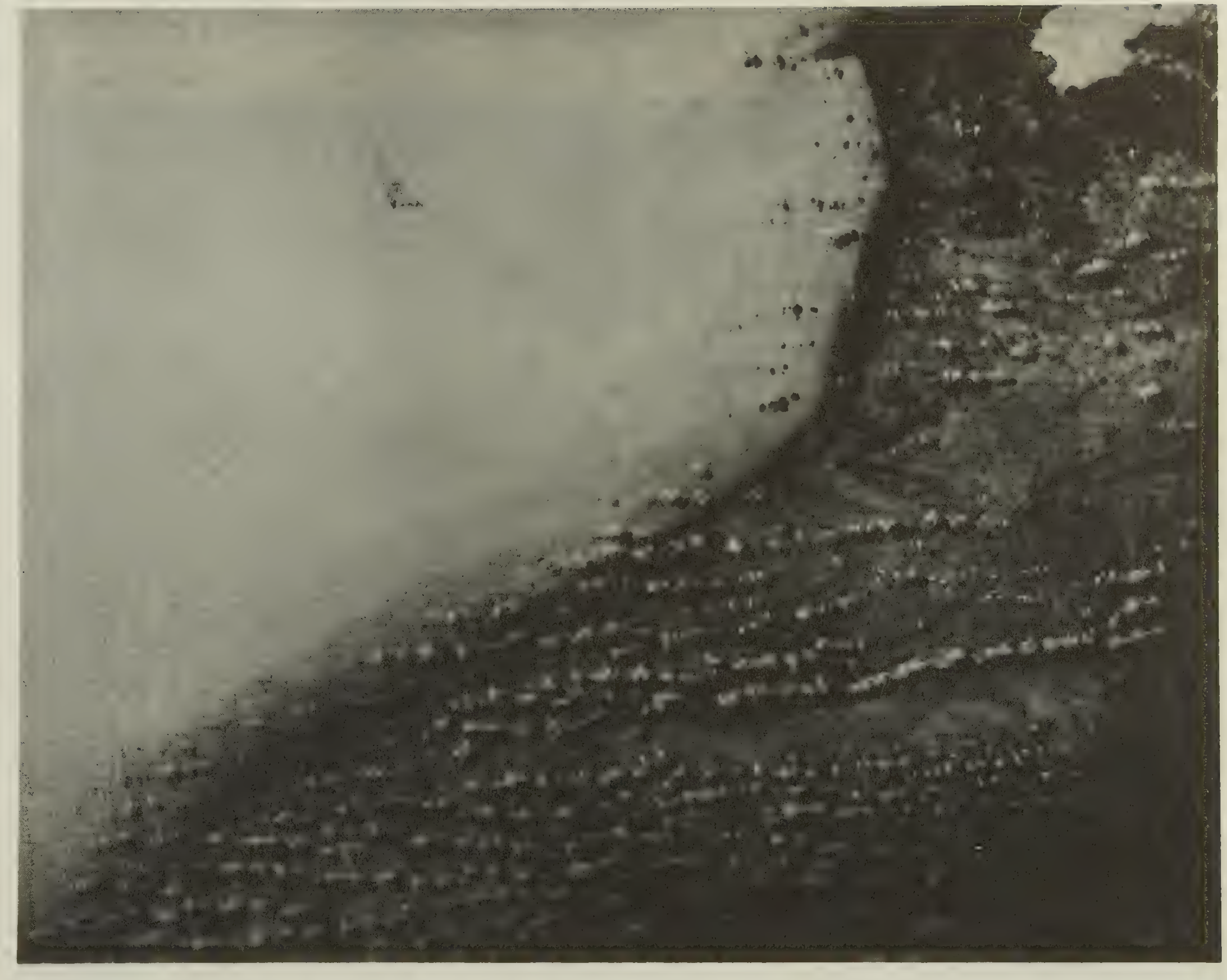

Fig. 4 b LANDSAT image of the Guajira coast (MSS 4 band) for 19 January 1973. Recently upwelled water is visible as a light grey plume extending southwest of Cabo de la Vela.

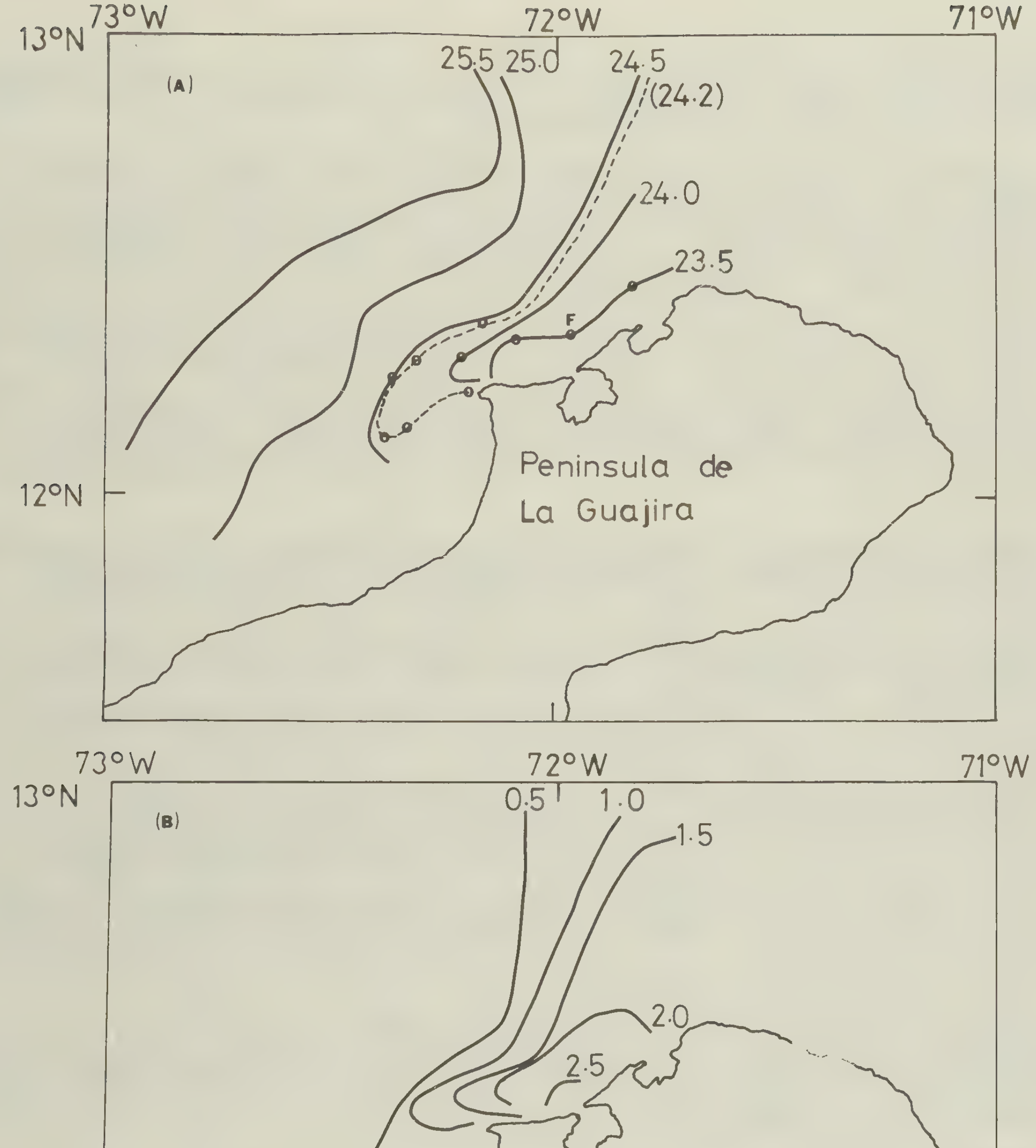
73°W
72°W
71°W
13°N
12°N
(A)
25.5
25.0
24.5
(24.2)
24.0
23.5
F
Peninsula de La Guajira
(B)
0.5
1.0
1.5
2.0
2.5

Fig. 5 Conditions of the plume of upwelled water off Cabo de la Vela during May, 1973.
(a) Surface temperature distribution (°C). Circles indicate points at which strong temperature discontinuities were encountered. Location of the front illustrated in Fig. 3 is indicated by the letter F;
(b) Surface chlorophyll a distribution ($mg \cdot m^{-3}$) as determined with a recording flow-through fluorometer.

receiving stations. The CICAR area is covered by two such stations, one at Greenbelt, Maryland, and the other at Cuiaba, Brazil. The former is operated by NASA, the latter by the Brazilian Instituto de Pesquisas Espaciais.

Considerable effort has been directed toward the use of LANDSAT-MSS data in detecting chlorophyll (and consequently, phytoplankton) distribution in surface waters. Strong (1974) found such applications useful in the study of phytoplankton in North American lakes. In the CICAR area, Maul (1973) has applied LANDSAT imagery to the study of the "loop current" in the Gulf of Mexico. A feature which Maul has termed the "edge effect" is the bright delineation of the loop current which appears in imagery from certain MSS bands. One of the major contributors to this edge effect is the phytoplankton which becomes concentrated in the area of discontinuity as a consequence of prevailing boundary layer dynamics. The green shift caused by chlorophyll reflectance is readily observable in images from the MSS 4 band (0.5-0.6 µm). Pingree et al. (1975) have recently studied the dynamics of processes by which phytoplankton becomes concentrated along oceanic frontal zones in the English Channel. They point out that these zones provide optimal conditions for the occurrence of phytoplankton blooms.

Frontal zones are also observable in the Guajira upwelling. Fig. 3 is a reproduction of continuous traces of surface chlorophyll a concentration and temperature across a front between offshore surface waters and recently upwelled waters. A peak in chlorophyll concentration coincides with the temperature discontinuity which marks the front. Fig. 4 illustrates the versatility of LANDSAT imagery in detecting and recording changes in these marine features. In the Colombian Caribbean, a centre of upwelling occurs to the northeast of Cabo de la Vela. Upwelled waters drift to the west and form a distinct plume due to the prominent obstruction of Cabo de la Vela. Images in the MSS 4 band (0.5-0.6 µm) for 01 and 19 January 1973 show the changes in the plume after an 18-day period. The biological significance of this plume is borne out by our observations aboard R/V JAMES M. GILLISS in May 1975. Fig. 5(a) depicts the temperature field as recorded with a thermistor thermometer. Points where abrupt temperature discontinuities were encountered clearly delineate the plume of cold water. Chlorophyll distribution, which was documented using a recording flow-through fluorometer, is influenced greatly by the presence of this nutrient-laden water; Fig. 5(b). The plume appears to be a semi-permanent feature, since we have detected its presence in the months of January, May and July. Fajardo (1975) also reports such a plume for September 1972.

These examples attest to the power of LANDSAT imagery in monitoring ocean resources. Unfortunately, quantification of suspended phytoplankton is difficult due to the relative insensitivity of the present MSS equipment. An instrument with greater dynamic range in the bands applicable to ocean sensing, the Coastal Zone Color Scanner, will be included in the sensor array of NIMBUS G, to be launched in 1978.

5. ACKNOWLEDGEMENTS

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SEX RATIO AND LENGTH-SEX COMPOSITION OF THE CAMPECHE-BANK LITTLEHEAD PORGY (CALAMUS PRORIDENS, JORDAN AND GILBERT, 1884) POPULATION

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CONTENTS

1. INTRODUCTION
2. METHODS
3. RESULTS
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Abstract

The study of the length-sex composition of the littlehead porgy of the Campeche Bank Gulf of Mexico, showed female preponderance (the sex ratio is 1♂ : 2.7♀ among adult fish). Females only were encountered among fish of the smallest length groups and males only among the largest.

Proterogyny as a form of nonfunctional hermaphroditism is an explanation of this sex-ratio peculiarity and length-sex composition. Mass female sex inversion was revealed in fish of 24 cm length.

According to D.F. Zamakhaev (1959) the length-sex composition of the littlehead porgy was classified as the third type which can be characterized by the following features: female dominance in fish of small length groups, gradual decrease in female ratio with increase in length and the fact that males attained a greater size.

It is considered that the significant female preponderance in the young age groups, which are always the most numerous in the population, is an adaptation which increases the reproductive ability of the species and results therefore in great abundance.

Resumen

El estudio de la composición por tallas y sexos de la población de C. proridens del Banco de Campeche, en el Golfo de México, ha revelado un predominio de las hembras (la relación de sexos entre los adultos es 1♂ : 2,7♀). Sólo se encontraron hembras entre los peces de menor talla y machos entre los de mayor talla.

La razón de esta particularidad en la proporción de los sexos y en la composición por tallas y sexos ha de buscarse en la proteroginia, forma de hermafroditismo no funcional. En peces de 24 cm de longitud se observó inversión masiva del sexo de las hembras.

Según D.F. Zamakhaev (1959), la composición por tallas-sexos de la población de C. proridens pertenece al tercer tipo, que puede caracterizarse por los siguientes rasgos: predominio de las hembras entre los peces de menor talla, disminución gradual de la proporción de hembras a medida que aumenta la talla, y mayor talla de los machos.

Se estima que el notable predominio de las hembras en los grupos de peces jóvenes, que son siempre los más numerosos en la población, representa una adaptación que aumenta la capacidad reproductiva de la especie y determina, así, una gran abundancia de la misma.

1. INTRODUCTION

The sex structure and length-sex ratio are adaptive features specific to different species and can be an objective criterion in an ecological analysis of populations. They are also of great importance for characterizing a type of commercial stock dynamics (Lapin, 1971; Makeeva and Nikolsky, 1965; Nikolsky, 1974; Salekhova, 1966, 1970; Zamakhaev, 1959). The problem of relative abundance and size composition of fish of different sexes in sparid populations inhabiting the Western Atlantic has not yet been dealt with except for Calamus bajonado (Dubovitsky, 1976a). The aim of the present paper is to consider the pecularities of sex composition of a C. proridens population - the most abundant sparid in the waters of the Campeche Bank - to trace its dynamics in accordance with fish size and to find out the determining cause of this biological peculiarity.

2. METHODS

Data from biological analyses carried out from May 1969 to August 1971 were used in the present paper. The investigational methods did not differ from those which were described earlier (Dubovitsky, 1976). About 800 individuals of C. proridens were analysed. All specimens subjected to the analysis according to sex were divided into three size groups: small specimens up to 20 cm long, medium 21-25 cm long and large, over 26 cm.

In addition to requirements for microscopical analysis, samples of gonads of varying maturity stages were taken from fish of different sizes. Irrespective of the development stage of the gonads, their parts were fixed in 4% or 10% formalin solution and Bouins. Further treatment of samples and histological preparations followed common methods (Roskin and Levinson, 1957). Sections were stained with Heidenhain's haematoxylin or, in some cases, according to Mallory. Thirty gonad preparations, 24 of them female, taken from fish 19-28 cm long, were investigated histologically.

3. RESULTS

During the investigations of 1969-71, irrespective of time and location, females predominated everywhere. The length distribution of both sexes is shown in Fig. 1A according to the three size range divisions given above. In Fig 1B the percentage length distribution of both sexes combined is shown, again according to the three size range divisions given above. When comparing the length frequency distribution of the different sexes it is clear that, in all specimens up to 23 cm long, males are very rare, i.e., only 1%. From 24 cm length upward the percentage of males increases sharply, forming 69% of the total. Fig. 2 shows the overall sex ratio of the entire size range, showing clearly the increase of the percentage of males with increasing length. Table I shows a breakdown into the three size groups specified above.

Although the sex ratio in any size group is not constant in different years, the general tendency of sex changes during a year's cycle (spawning, feeding, etc.), is obvious and constant. Invariably, with increasing length of the fish, the percentage of females decreases considerably. Only females are to be seen among the smallest specimens, and among the largest, only males. Overall the dominance of females amounted to 73%. This is characteristic of the whole commercial population and the sex ratio here is 1♂ : 2.7♀. Additionally the relationship between the frequency of females and length is clear since the dotted field shown in Fig. 3 approximates to a straight line expressed by the following equation:

$$S = 2.338 - 0.072\ L \text{ where}$$

S - percentage of females
L - mean length of females in sampling

Thus the sex ratio changes regularly with size and this change is expressed by reverse dependence.

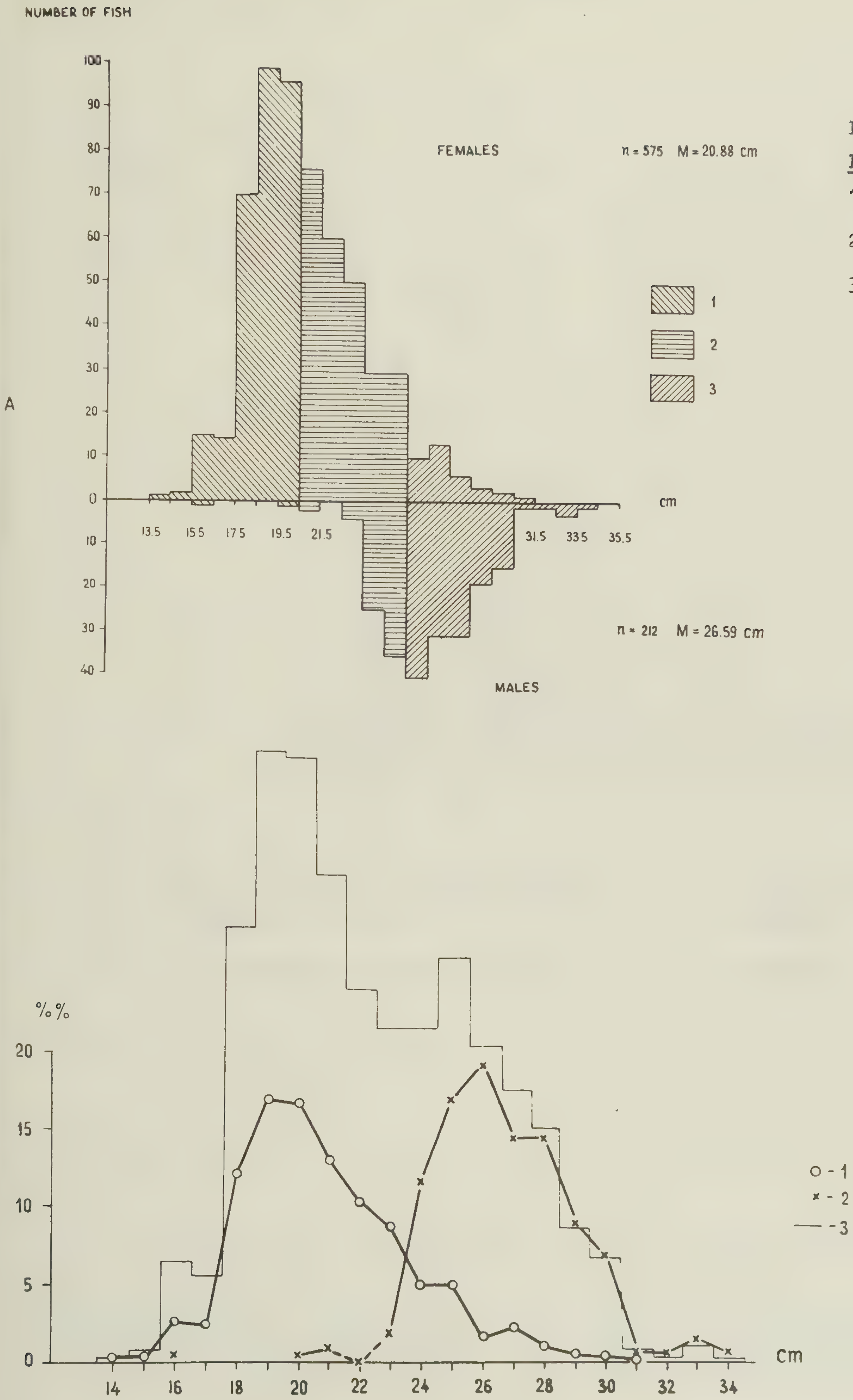


Fig. 1A Key

Number of individuals

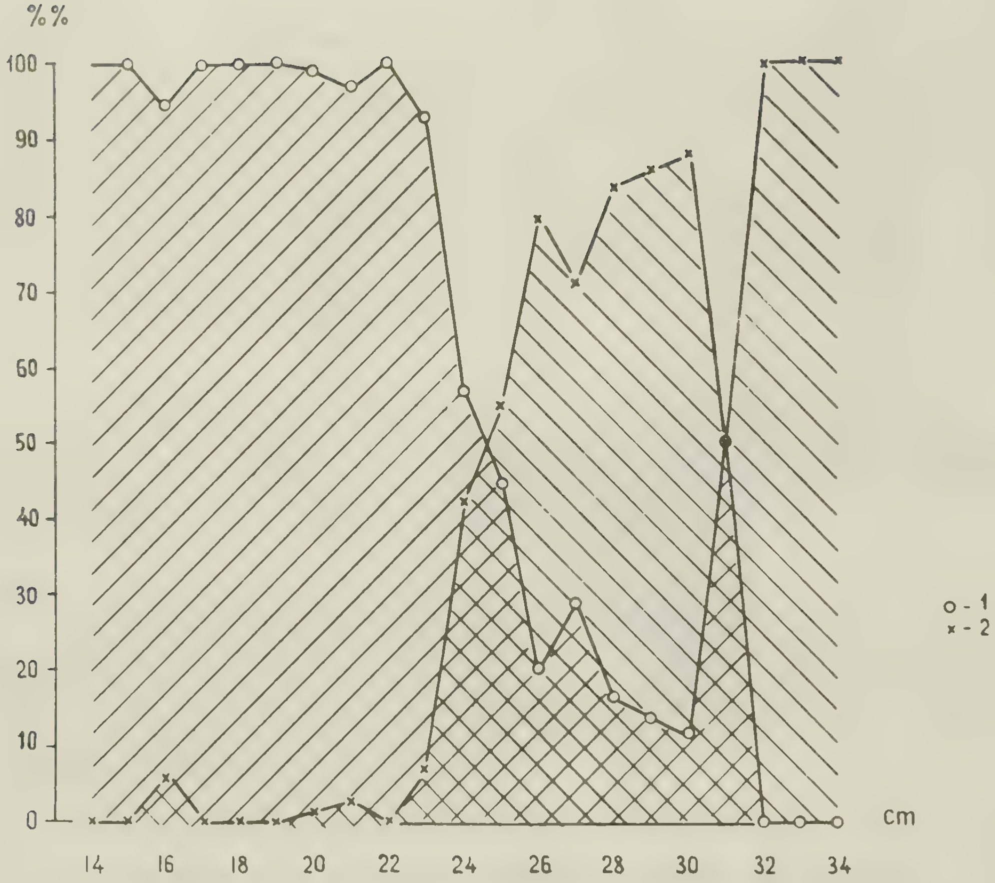
1. Among small specimens
2. Among medium specimens
3. Among large specimens

Fig. 1B Key

In %

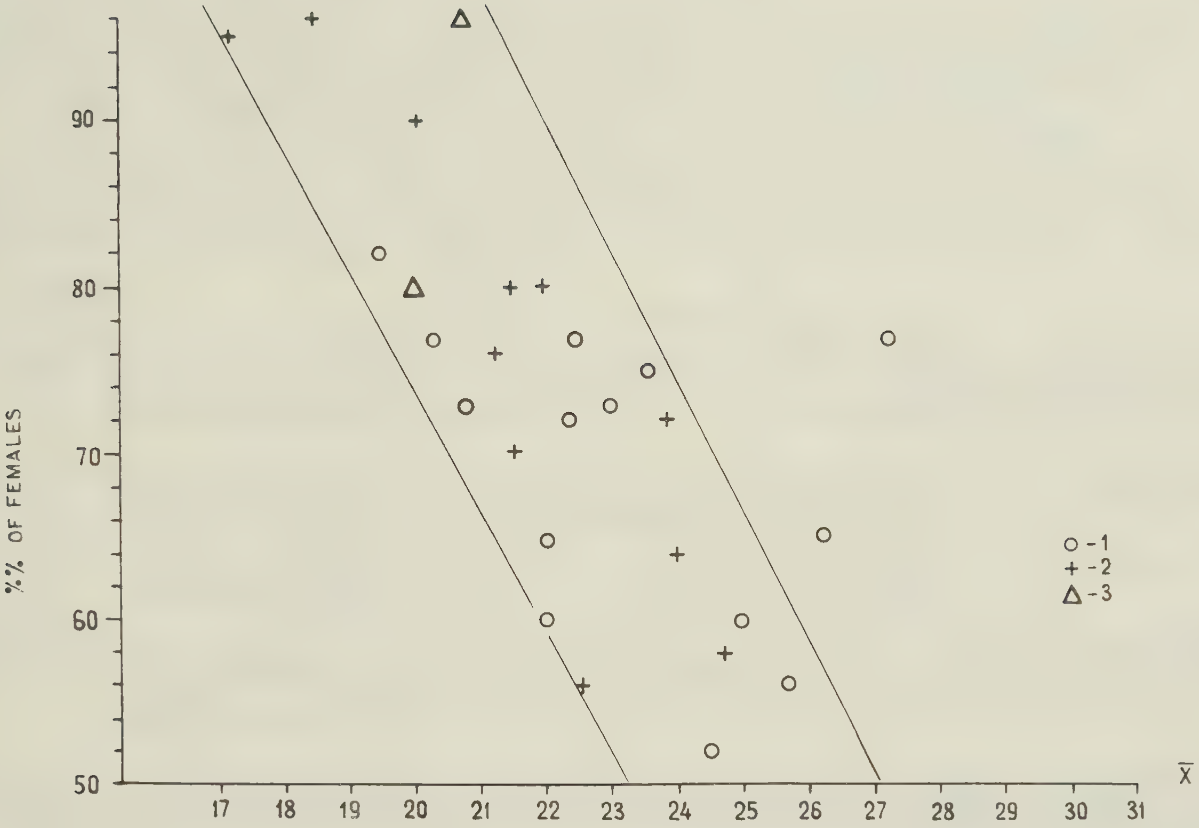
1. Females
2. Males
3. Total number

Fig. 1 The length distribution of females and males of the *C. proridens* commercial population



Key: 1 – Females; 2 – Males

Fig. 2 The overall sex ratio in the whole commercial population



Key: 1 - In December-March; 2 - In June-August; 3 - In November

Fig. 3 The mean length (X) of females sampled and their frequency in the sexually mature part of the C. proridens population during the sampling period 1969-71

TABLE I

Percentage of females in the three different size ranges in the sexually mature part of the commercial catch of *C. proridens* taken from the Campeche Bank during the sampling period 1969-71

Size group cm	Percentage of females	n %a/
Small 14-20	99.3	298 37.9
Medium 21-25	78.5	311 39.5
Large 26-34	19.7	178 22.6
In the commercial part of the population	73.1	787 100

a/ In % of the total number of analysed specimens

Preliminary histological investigations of gonad sections indicate that, in the ontogenesis of *C. proridens*, there is a successive sex inversion from female to male, i.e., proterogyny is shown as a form of nonfunctional hermaphroditism, the majority of young fish functioning as females with a subsequent transformation of many into males. Although the size of females at which the ovary regresses and the testis develops is very variable, a pronounced sex inversion is observed at a length about 24 cm (Figs. 1A, 1B, and 2).

During the size composition investigations of *C. proridens* it was noted that the different length characteristics of females and males are statistically valid and sufficiently great to qualify as sexual dimorphism (Dubovitsky, 1976b, Fig. 5). The smaller size of the female is considered to be a regular consequence of proterogynous hermaphroditism and can be explained by a specific metabolism during the early stages of ontogenesis. Much energy expenditure is necessary to develop a great quantity of oöcytes within the spawning period. This slows down the rate of linear growth. The modal female group is 18-21 cm long (59% of all females). According to N.J. Lipskaya the amount of energy expended in the formation of the many egg developmental stages in *Mullus barbatus ponticus* Essipov during the spawning period is 40-60 times greater than the energy expenditure on growth during the same period (Lipskaya, 1967).

Subsequent to sex inversion in specimens which begin functioning as males this metabolic ratio changes and the rate of growth increases. The modal male group is 25-28 cm long (65% of all males).

Proterogyny as a form of normal sex development is rather widely distributed among fish and noted in many species, the number of known examples now increasing gradually. However, among the proterogynous hermaphrodites, the sex structure of populations and length ratios are known for a few species only, namely *Spicara smaris* (Lozano Cabo, 1953; Probatov and Moskvin, 1940; Reinboth, 1962; Salekhova, 1966; Smirnov, 1959; Zamakhaev, 1959) *Pagellus erythrinus* (D'Ancona, 1949; Reinboth, 1962; Rijavec and Zupanovič, 1965; Zei and Zupanovič, 1961), *Spicara chryselis* (Nullo, 1959; Planes y Vives, 1955), *Spicara maena* (Nullo, 1959; Reinboth, 1962) and *Calamus bajonado* (Dubrovitsky, 1976a).

Similar to the above species, by virtue of the length-sex ratio, C. proridens from the Campeche Bank, as classified by D.F. Zamakhaev, is referred to the third type; this is characterized by the preponderance of females among the mature fish, this preponderance decreasing with increasing size, resulting, eventually, in male preponderance among the largest fish.

The importance of proterogynous hermaphroditism as an adaptation for maintaining the maximum abundance possible by a high rate of reproduction is clear, but the biological mechanism of this phenomenon is not always clear and is difficult to explain fully (Alekseev, 1969; Nikolsky, 1974; Salekhova, 1970).

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DISTRIBUTION, MIGRATIONS AND SOME BIOLOGICAL FEATURES OF LITTLEHEAD PORGY (CALAMUS PRORIDENS, JORDAN AND GILBERT, 1884) FAMILY SPARIDAE, OF THE GULF OF MEXICO

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Abstract

Material collected during the joint Soviet-Cuban investigations of 1969-71 show C. proridens to be the most abundant representative of the genus inhabiting the shallow plateau of the Yucatan Peninsula down to 50-55 m depth; during some periods it forms commercially exploitable concentrations. A peculiarity of size distribution of such a concentration is the presence of sexual dimorphism, i.e., females are smaller than males. Females 18-22 cm long dominate the catches.

Spawning is partial and seasonal, from December to August, occurring in different areas of the Bank, but always in the offshore part. Mass spawning of large fish is marked in January-March in the east and north-west of the Bank, small fish spawning in the central part during May-June. Although of some duration, the spawning period coincides with favourable conditions for the normal development of the early pelagic stages.

The habitats of young, immature and adult fish differ. Migrations of mature fish are pronounced during the spawning period; they move offshore to spawn and back to shallow waters to feed during the interspawning period.

Feeding is mainly on crabs and bivalve molluscs. Fat is accumulated in the ventral cavity, peaking at the beginning of the spawning period. These fat reserves are utilized for the development of the sexual products.

It is the differences in spawning periods, fat accumulation dynamics and feeding intensity of mature fish of different sizes which determine the different rhythms of annual cycles and the complex structure of the commercial population.

Resumen

El material obtenido en las investigaciones conjuntas soviético-cubanas realizadas en los años 1969-71, han permitido establecer que el pez más abundante del género Calamus en las aguas del Banco de Campeche es *C. proridens*. Se ha determinado la dominancia en abundancia del pez de pluma hasta una profundidad de 50-55 m. Estos ocurren en densas concentraciones que fluctúan estacionalmente.

La estructura de la población comercial presenta una característica peculiar de dimorfismo sexual basada en la diferencia en tallas. Los machos son más grandes que las hembras, entre las cuales la talla de 18 a 22 cm predomina.

El desove de *C. proridens* es estacional. Ocurre en las distintas partes del Banco desde diciembre hasta agosto, siempre lejos de la costa. El desove principal de los peces grandes tiene lugar durante los meses enero a marzo en la parte oriental y norte-occidental del Banco. El de los peces de tamaño pequeño se observa durante mayo a junio en la parte central. Aunque es bastante larga, la estación de desove coincide con las condiciones favorables para el desarrollo de los huevos y larvas, los cuales son pelágicos.

Los lugares donde habitan los peces jóvenes, inmaduros y adultos son diferentes.

Las migraciones de los peces maduros son más frecuentes en la temporada de desove cuando la masa de *C. proridens* se va más lejos de la costa para desovar, regresando luego a la zona costera (migración inter desove y de alimentación). Los peces adultos se alimentan principalmente de braquiuros y bivalvos.

La maxima cantidad de grasa intestinal se acumula en los principios de la estación de desove y después se consume para producir productos sexuales.

Las diferencias en el tiempo de desove, en la dinámica de la acumulación de grasa y en la intensidad de la alimentación de los peces maduros de diferentes tallas determinan diferentes ritmos de ciclos anuales y la estructura compleja de la parte comercial de la población.

1. INTRODUCTION

The sparids of the western Atlantic number about 25 species (Druzhinin, 1976). *Calamus* is the most abundant genus and is of direct interest to commercial fisheries development in tropical and sub-tropical areas; however the biology of the species of this genus, *C. bajonado* excepted (Dubovitsky, 1974a), had not been studied prior to this paper.

New data, resulting from the joint Soviet-Cuban fisheries investigations in the Caribbean area between 1969 and 1971, have resolved a number of problems concerning the biology of species of *Calamus*. This paper examines material which has resulted from seasonal trawling surveys and presents findings concerning the biology of *C. proridens*. Sampling methods and data processing are as used before (Dubovitsky, 1974). Relevant information is given in Table I; station locations are shown in Fig. 1.

TABLE I

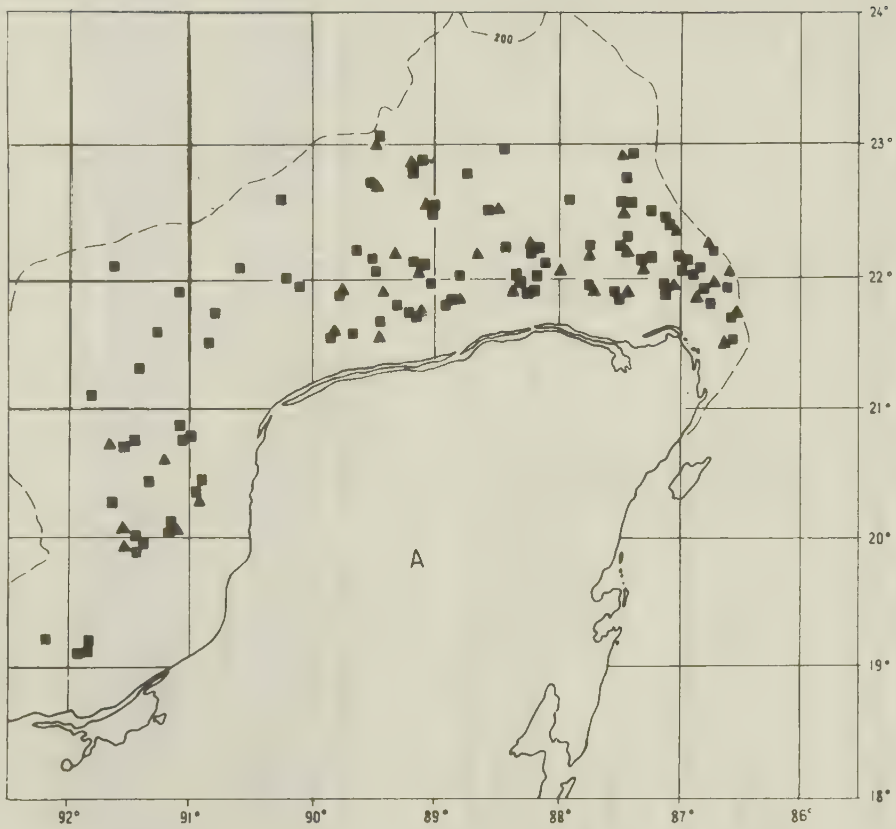
Number of hauls and fish analysed

Time	Hauls	Fish measured	Fish analysed
1969			
May-June	34	138	30
July	29	-	25
August	42	189	30
	105	327	85
1970			
January	37	615	135
July-August	-	266	120
November-December	54	2 115	98
	91	2 996	353
1971			
February-March	39	2 499	256
July-August	44	466	135
	83	2 965	391
Total, all years:	279	6 288	829

2. DISTRIBUTION

In earlier works (Jordan and Evermann, 1898; Breder, 1929) distributional boundaries of *C. proridens* were vaguely referred to as the Antillean shelf. Later, it was reported from the western part of Haiti (Beebe and Tee-Van, 1928), indicating a discontinuity in the Gulf area (Duarte-Bello, 1959). According to recent works (Randall and Caldwell, 1966; Randall, 1968), the Campeche Bank appears to be the southern limit of its range.

A review of the literature, coupled with our own observations, indicates the habitat of *C. proridens* to be geographically small, ranging from 35° N, on the eastern shelf of North America, to 20° N, the Campeche Bank. It is absent from the western part of the Gulf of Mexico. Published works referring to the south-west coast of Florida indicate it is most


200
A
24°
23°
22°
21°
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19°
18°
92°
91°
90°
89°
88°
87°
86°

Fig. 1A Study area and station locations on Campeche Bank during the months November-March 1969-71. (Squares refer to January and November-December 1970, triangles refer to February-March 1971)

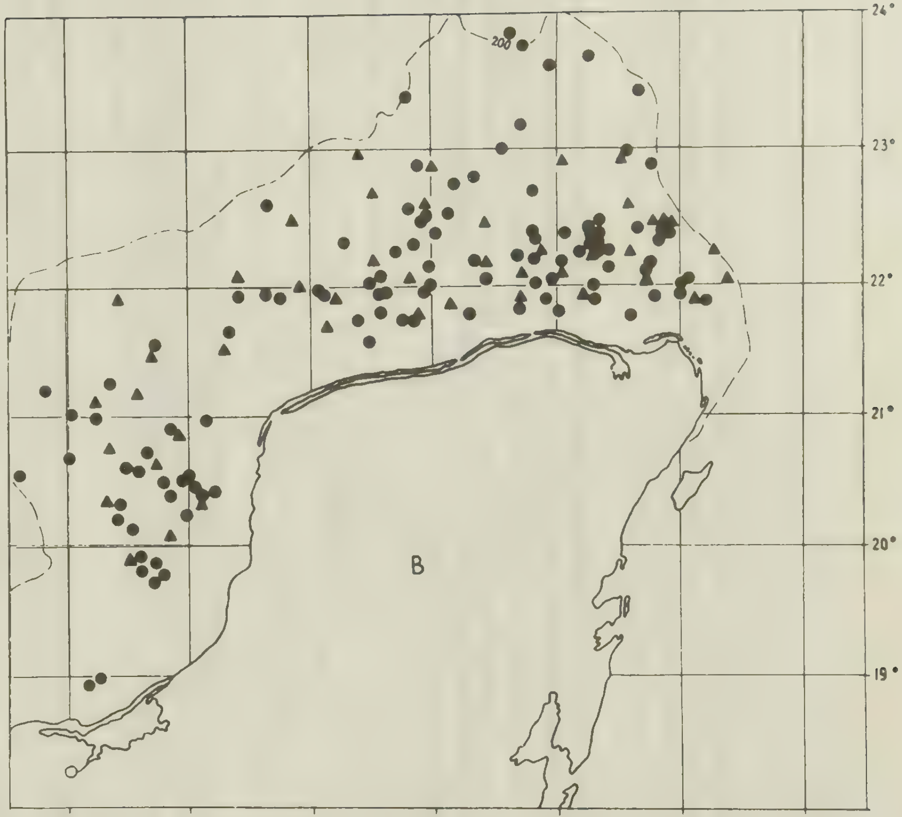

200
B
24°
23°
22°
21°
20°
19°
92°
91°
90°
89°
88°
87°
86°

Fig. 1B Study area and station locations on Campeche Bank during the months May-August, 1969-71. (Circles refer to May-August 1969, triangles refer to July-August 1971)

Figs. 2A-F Distribution of bottom temperatures and *C. proridens* catch rates, by month, 1969-71. (Open symbols represent catches in depths <35 m, solid symbols catches in depths >35 m

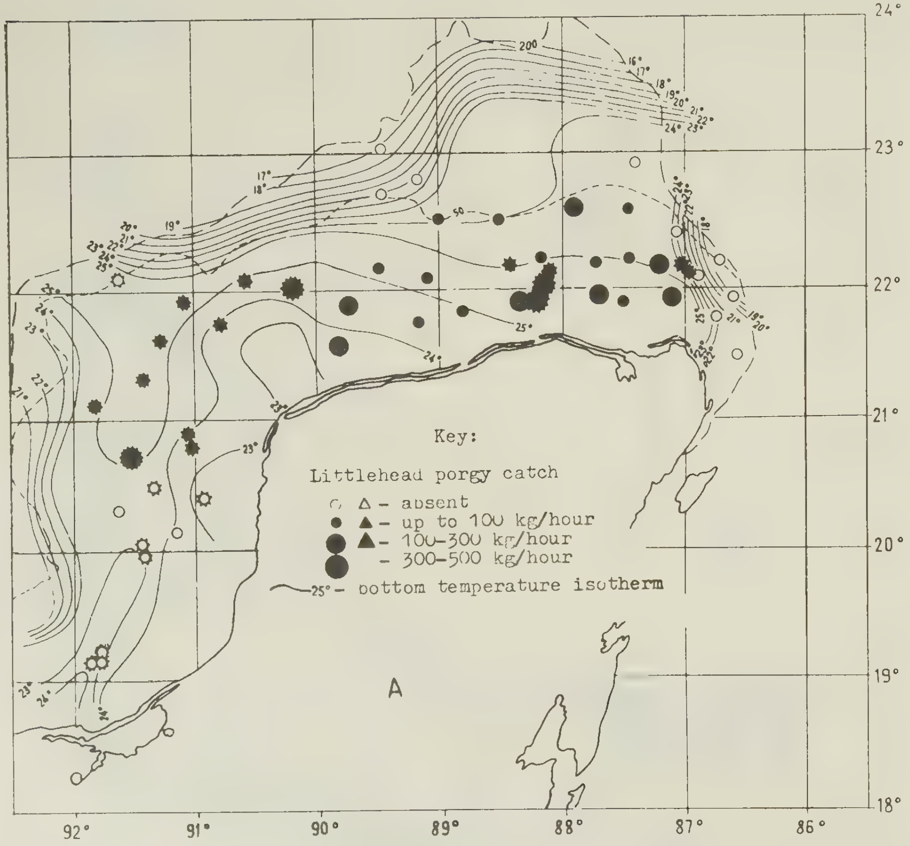
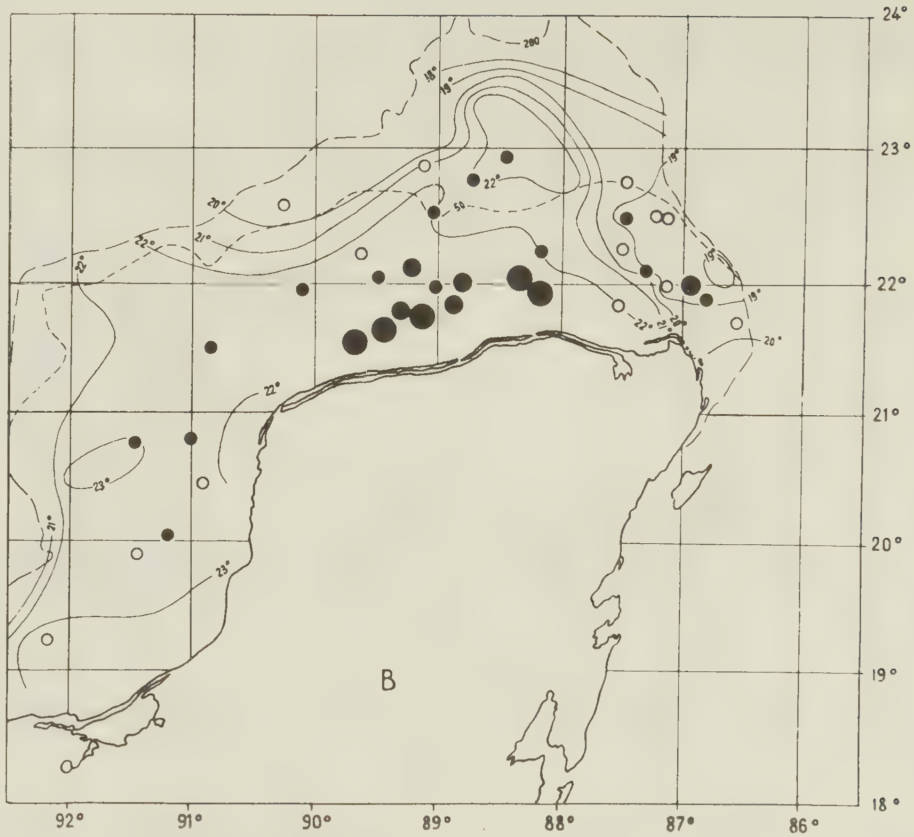

24°
23°
22°
21°
20°
19°
18°
92°
91°
90°
89°
88°
87°
86°
200
50
Key:
Littlehead porgy catch
○ △ - absent
● ▲ - up to 100 kg/hour
● ▲ - 100-300 kg/hour
● - 300-500 kg/hour
25° - bottom temperature isotherm
A

Fig. 2A November (circles) and December (triangles) 1970. Temperatures shown are for November


24°
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88°
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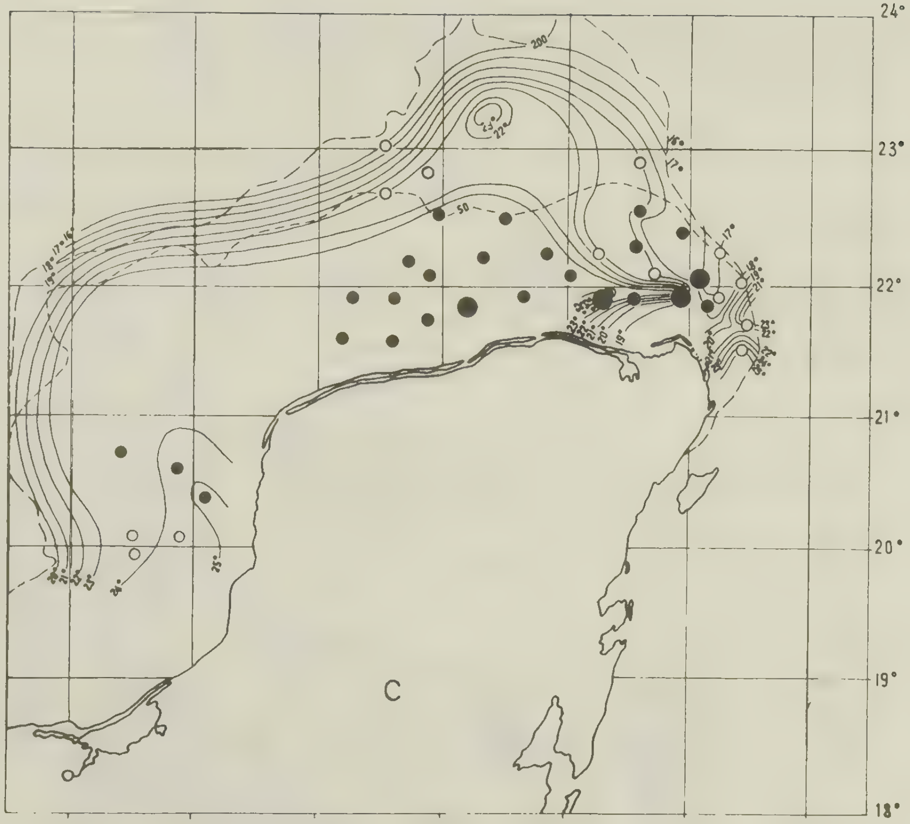
Fig. 2B January 1970


24°
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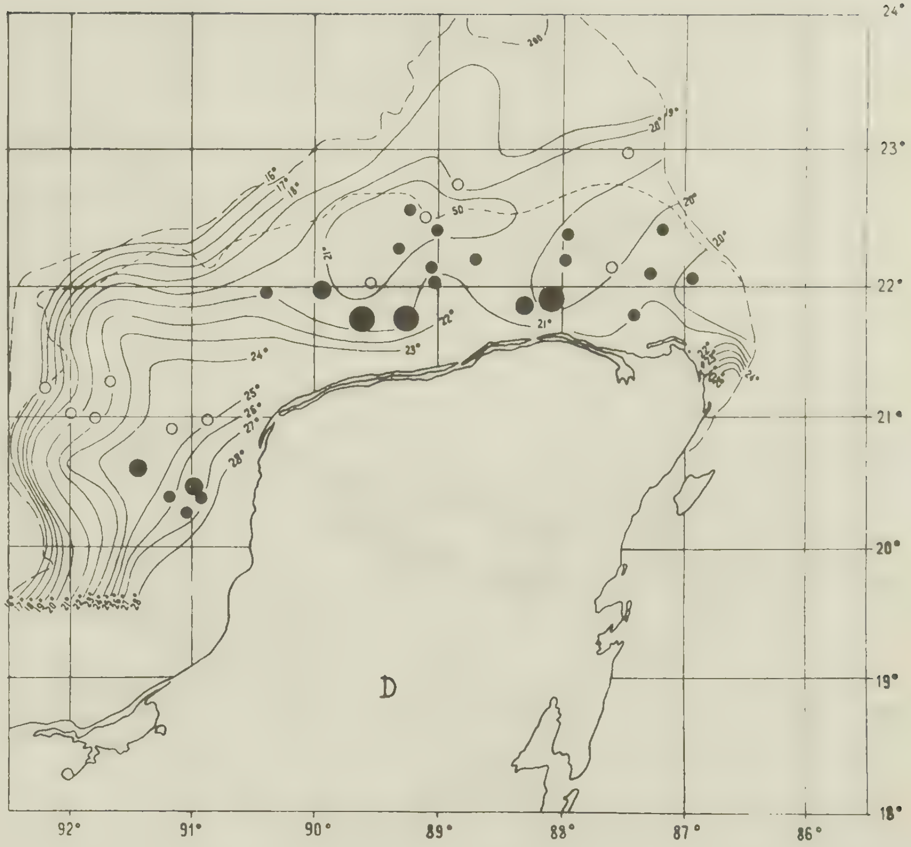
C

Fig. 2C February-March 1971


24°
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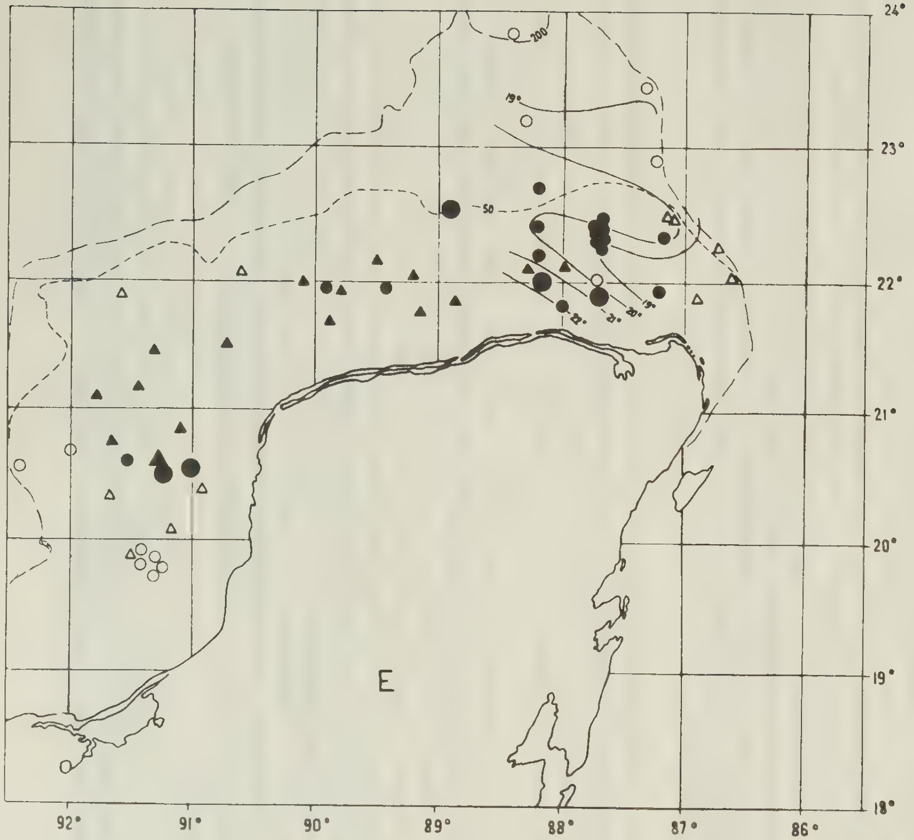
D

Fig. 2D May 1969


E
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19°
18°
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89°
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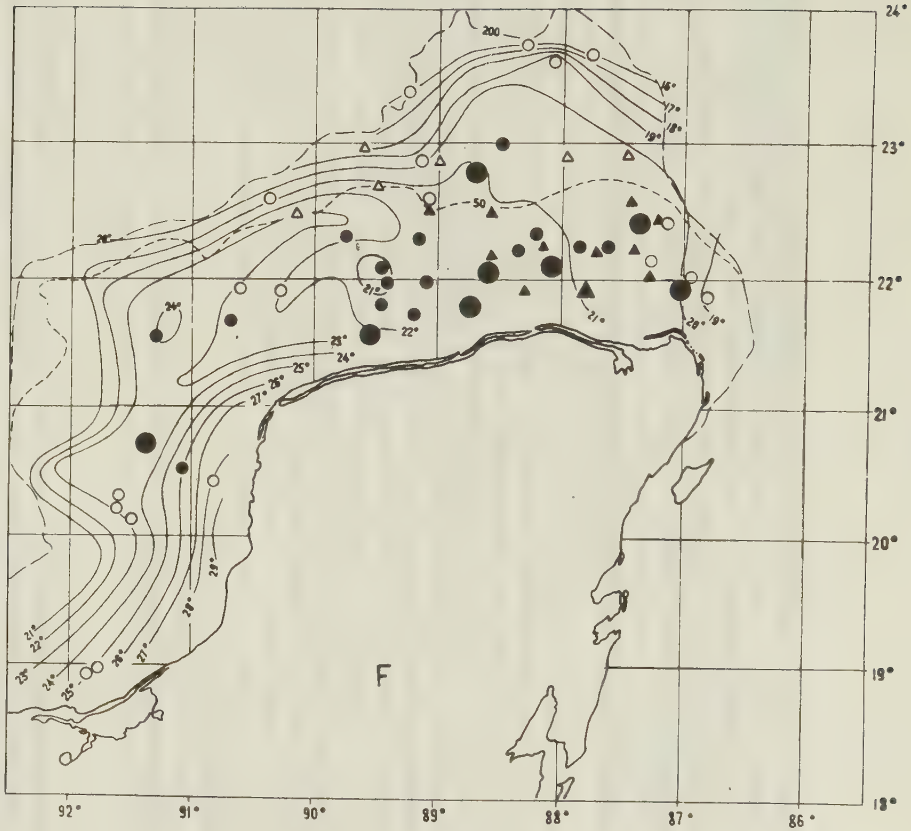
87°
86°

Fig. 2E June 1969 (circles) and June 1971 (triangles).
Temperatures shown are for June 1971


F
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21°
20°
19°
18°
92°
91°
90°
89°
88°
87°
86°

Fig. 2F August 1969 (circles) and August 1971 (triangles)
temperatures shown are for August 1969

common down to a depth of 60 m (Jordan and Evermann, 1898; Breder, 1929; Beebe and Tee-Van, 1928; Randall and Caldwell, 1966). As a last point, it has now been established that C. proridens is the most abundant species of the genus and, on Campeche Bank, by virtue of its abundance, it is considered by us to be the most important demersal species. It can be noted here that C. proridens yielded over 500 kg/h trawling from a research vessel.

2.1 Variations in Seasonal Distribution and Analyses of Commercial Concentrations

The temperature régime in the area under study is, for the most part, governed by the seasonal penetration, to varying degrees, of cold, deep water into the shallow plateau area. The greatest penetration is in the spring-summer period (Bessonov *et al.*, 1971; Bogdanov, 1965; Bogdanov *et al.*, 1967; Dubovitsky, 1974; Jrómov, 1965,1967; Vasiljev and Torin, 1965), and it is in this period that the bottom temperature is at its minimum. Maximum bottom temperature is in November (Bessonov *et al.*, 1971; Bogdanov, 1965; Dubovitsky, 1974; Salnikov, 1965; Vasiljev and Serrano, 1974). It is interesting that the bottom water temperature régime does not correspond generally with the climatic régime; thus the bottom water is at its coldest between May and August, and at its warmest between September and November/December. There is an intermediate period between December and March/April, the cold water not penetrating further than 88°W, when there is some correspondence with the climatic régime. Supporting data for the period 1966-72 are given in Vasiljev and Serrano (1974) and, for 1969-71, in Dubovitsky (1974).

The relationship between C. proridens distribution and the temperature régime is as follows:

December-March

Despite the transition from warm to cooler bottom water, the area over which C. proridens was found did not change significantly (Fig. 2a-c). Only in January, when the bottom water temperature did not exceed 22°C, did C. proridens extend beyond the limits of the shallow plateau down to a depth of 65-70 m and as far south as 20°N (Fig. 2b).

The quantitative distribution within the area varied significantly. In December, more C. proridens were taken in the coastal waters of the eastern part (up to 88°W) and in the western part (91°W) of the Bank, at the edge of the shallow plateau (Fig. 2a). In January the bulk of the population was found in the central zone, dense concentrations being found within 88°W - 90°W (Fig. 2b). In February-March it was most abundant in the coastal area of the eastern area (up to 89°W) down to 25 m, but extending to 40 m in the zone of the cold water inflow (Fig. 2c).

Thus, during the period December-March, the majority of mature fish migrate into the coastal waters of the central part (January), with subsequent dispersion and a gradual shift eastward (March).

May-August

On the greater part of the plateau, up to 90°W, relatively low bottom temperatures of 20-22°C were noted while in the west and south-west of the area, south of 22°N, temperatures were 24°C-25°C.

At the beginning of the period May-June the area inhabited was restricted to the shallow plateau (Fig. 2d). In August, despite similar temperature conditions, this area increased, and considerable numbers of C. proridens were found beyond the limits of the plateau, down to depths of 60-85 m (Fig. 2f). Commercially exploitable aggregations were observed only in May-June; these were in the same areas and at the same depths as the January aggregations (Fig. 2d). At the end of this period, i.e., August, C. proridens is most abundant east of 89° 30'W, below 30 m (Fig. 2f).

November

Bottom temperature reaches its maximum in November and the beginning of December, but did not affect the distribution of C. proridens; as before, it was taken everywhere within the limits of the shallow plateau, commercially exploitable aggregations being found only in the eastern and western parts (Fig. 2a).

Over the periods noted above, the temperature range of the area inhabited by C. proridens is fairly large, 17°C-27°C. Even so, within the limits of the shallow plateau, there is considerable movement and, during certains periods, commercially exploitable aggregations occur in the coastal zone of the central part of the Bank. The formation of these aggregations coincides with the period of low bottom temperature.

3. SIZE DISTRIBUTION IN THE AGGREGATIONS AND SEXUAL DIMORPHISM

Size distribution of C. proridens within aggregations from different parts of the Bank is shown in Figs. 3 and 4 and Table II, From these data it is possible to note changes in size distribution during the year and to detect the movement of fish belonging to different size groups within the limits of the habitat.

For convenience, the fish will be divided into two general categories, small fish, <20 cm, and large fish, >20 cm.

December-March

Excepting the western part down to 35-40 m, large C. proridens predominated over virtually the whole area during December; in the east, in the zone affected by cold waters, they were 27-31 cm (Fig. 3a), in the north-west, 22-24 cm and 26-27 cm (Fig. 4a). Off-shore, at the edge of the shallow plateau, and in the south-west, south of 21°N, numbers of small fish (19-20 cm) increased (Figs. 4a,b).

In January, mostly small C. proridens are found in the central part of the Bank; here, fish 19-21 cm long were forming the basis of the exploitable aggregations. At the greater depths, as in December, only small fish of 18-19 cm were found (Fig. 3b). Over the remainder of the area large fish 21-23 cm long predominated, along with those of a larger size (Figs. 3b, 4a, b). At the same time, over the shallow part of the west, north-west and, particularly, the central zones, the appearance of small, immature fish 13-16 cm was observed.

In February-March, relative distribution changed again. Unlike previous months in the east of the Bank, and despite the similarity of temperature conditions, fish 20-23 cm long (Fig. 3a) constituted the main part of the catch. Over the whole shallow area of the central zone between 88°W and 90°W, down to 25-30 m fish between 16-29 cm were evenly distributed while, in the deeper water, 30-50 m, small fish 19-20 cm predominated as before (Fig. 3b).

The main trends are:

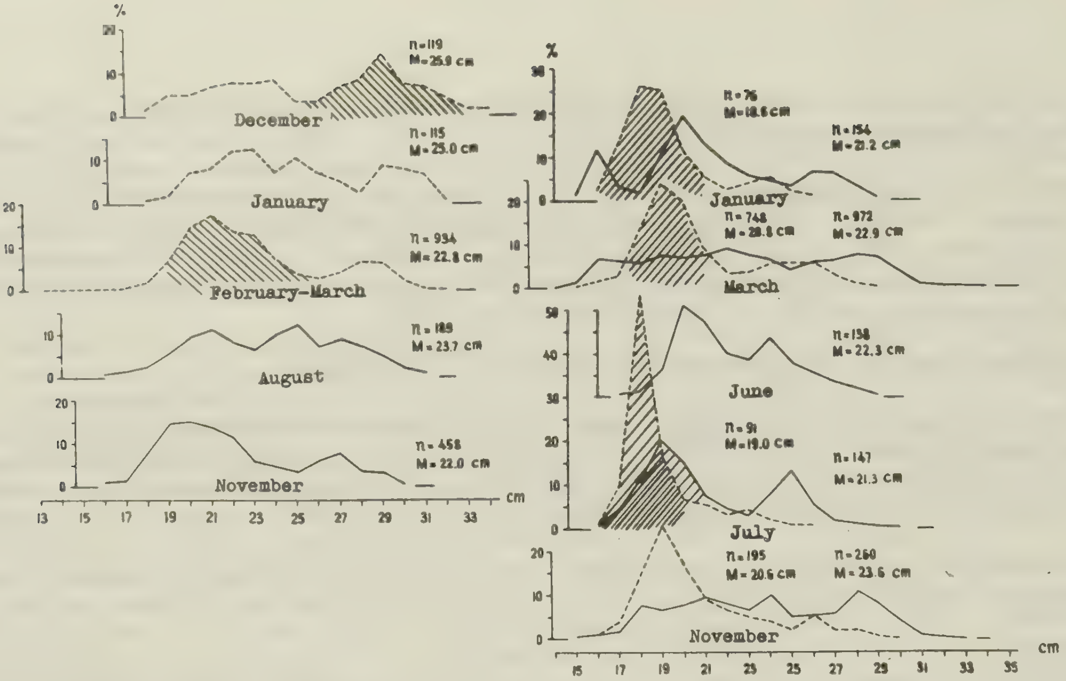
(1) In the east, over the area with relatively cold bottom water (Figs. 2a-c) large C. proridens were always present, but the numbers decreased gradually from December to March (Fig. 3a).

(2) Coastal water populations of the central zone down to 30-35 m show the greatest changes in size range; large fish are present in December, commercially exploitable small fish in January, with both size groups present in March.

(3) Over the off-shore part of the shallow plateau, between 35-55 m, small fish, 18-20 cm, dominated during the whole period, their numbers increasing with depth (Fig. 3b).

(4) Juvenile, immature fish of 13-16 cm appeared in inshore waters of the west and, in particular, the central part in January and in the east of the Bank in February.

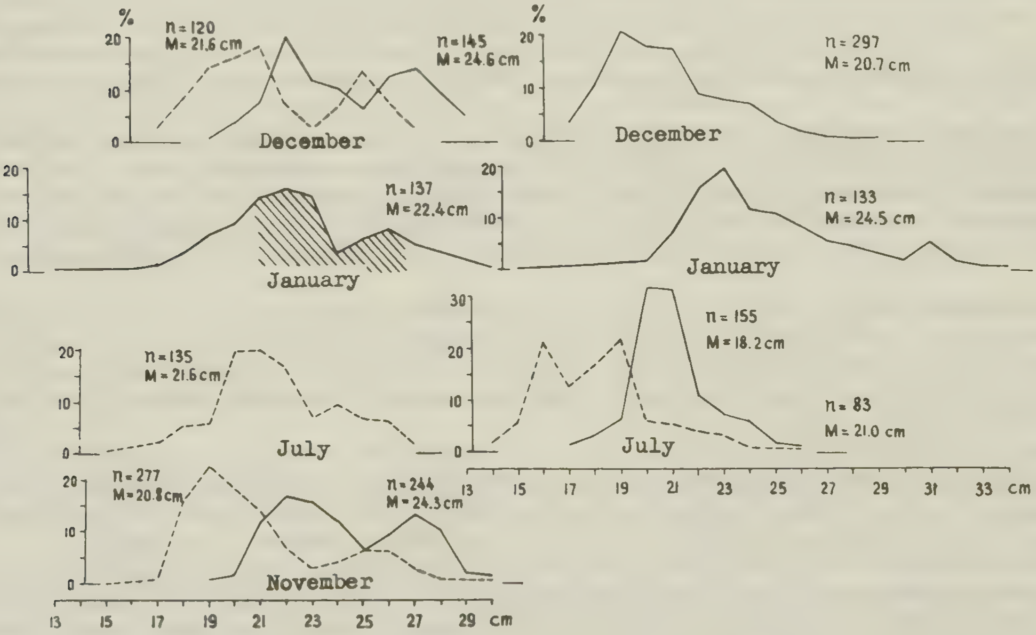
Data analysis between December and March shows that small fish move gradually from west to east. An extensive migration of 19-21 cm fish to the inshore waters of the central part during January forms the commercially exploitable concentrations. Movement of large fish from western and eastern zones to inshore waters of the central zone is pronounced in March.



A - eastern area

B - central area

Fig. 3 Size distribution of C. proridens on Campeche Bank for different months Solid lines represent depths less than 30-35 m; dashed lines represent depths greater than 30-35 m



A - north-western area

B - western area

Fig. 4 Size distribution of C. proridens on Campeche Bank for different months. Solid and dashed lines as in Fig. 3

TABLE II

C. proridens size composition in different areas of the Campeche Bank during the year
(Figures above lines refer to depths less than 35 m;
figures below lines refer to depths greater than 35 m)

Months	Size range (cm)	Modal group (cm)	Relative frequency of modal group (%)	Mean length (cm)	Percentage length distribution in sample		
					<20 cm	20–25 cm	>25 cm
EASTERN AREA							
December	$\overline{\text{18–34}}$	$\overline{\text{21–24}}$ 27–31	$\overline{30}$ 44	$\overline{25.9}$	$\overline{7}$	$\overline{39}$	$\overline{54}$
January	$\overline{\text{18–32}}$	$\overline{\text{22–23}}$ 29–31	$\overline{24}$ 24	$\overline{25.0}$	$\overline{3}$	$\overline{57}$	$\overline{40}$
February-March	$\overline{\text{13–32}}$	$\overline{\text{20–23}}$	$\overline{58}$	$\overline{22.9}$	$\overline{8}$	$\overline{70}$	$\overline{22}$
August	$\underline{\text{16–31}}$	20–22 $\underline{\text{24–25}}$	21 $\underline{22}$	$\underline{23.7}$	$\underline{11}$	$\underline{57}$	$\underline{32}$
November	$\underline{\text{18–30}}$	$\underline{\text{19–22}}$	$\underline{55}$	$\underline{22.0}$	$\underline{25}$	$\underline{54}$	$\underline{21}$
CENTRAL AREA							
January	$\frac{\text{15–29}}{\text{16–26}}$	$\frac{\text{19–22}}{\text{18–19}}$	$\frac{51}{51}$	$\frac{21.2}{18.6}$	$\frac{28}{67}$	$\frac{58}{30}$	$\frac{14}{3}$
March	$\frac{\text{14–34}}{\text{15–29}}$	$\frac{}{\text{19–20}}$	$\frac{}{43}$	$\frac{22.9}{20.8}$	$\frac{27}{42}$	$\frac{41}{47}$	$\frac{32}{11}$
June	$\underline{\text{16–29}}$	20–21 $\underline{25}$	$\underline{14}$	$\underline{22.3}$	$\underline{9}$	$\underline{79}$	$\underline{12}$
July	$\frac{\text{16–30}}{\text{16–26}}$	$\frac{\begin{array}{c}\text{18–20}\\\text{24–26}\end{array}}{18}$	$\frac{\begin{array}{c}47\\29\end{array}}{48}$	$\frac{21.5}{19.0}$	$\frac{37}{76}$	$\frac{53}{23}$	$\frac{10}{1}$
November	$\frac{\text{15–33}}{\text{16–30}}$	$\frac{}{\text{18–20}}$	$\frac{}{58}$	$\frac{23.6}{20.6}$	$\frac{18}{47}$	$\frac{47}{44}$	$\frac{35}{9}$
NORTH-WEST AREA							
December	$\frac{\text{19–29}}{\text{17–27}}$	$\frac{\begin{array}{c}\text{22–24}\\\text{26–27}\end{array}}{\begin{array}{c}\text{19–21}\\\text{24–26}\end{array}}$	$\frac{\begin{array}{c}42\\26\end{array}}{\begin{array}{c}48\\27\end{array}}$	$\frac{24.6}{21.6}$	$\frac{1}{26}$	$\frac{59}{64}$	$\frac{40}{10}$
January	$\underline{\text{13–30}}$	$\underline{\text{21–23}}$	$\underline{45}$	$\underline{22.4}$	$\underline{15}$	$\underline{65}$	$\underline{20}$
July	$\overline{\text{15–27}}$	$\overline{\text{20–22}}$	$\overline{55}$	$\overline{21.6}$	$\overline{15}$	$\overline{77}$	$\overline{8}$
November	$\frac{\text{19–30}}{\text{15–30}}$	$\frac{\begin{array}{c}\text{21–24}\\\text{26–28}\end{array}}{\text{18–21}}$	$\frac{\begin{array}{c}56\\32\end{array}}{56}$	$\frac{24.3}{20.8}$	$\frac{1}{40}$	$\frac{63}{51}$	$\frac{36}{9}$

Months	Size range (cm)	Modal group (cm)	Relative frequency of modal group (%)	Mean length (cm)	Percentage length distribution in samples		
					<20 cm	20-25 cm	>25 cm
SOUTH-WEST AREA							
December	17-29	19-21	56	20.7	34	63	3
January	15-34	22-23	35	24.5	3	66	31
July	17-26	20-21	63	21.0	11	88	1
	14-26	16-19	72	18.2	78	21	1

May-August

In May-June both the quantitative distribution (cf. Figs. 2d and 2b) and the size distribution (Fig. 3b) of *C. proridens* are similar to those in January.

During this period the same general distribution of large and small fish could be noted. The main movement of small fish, i.e., from west to east, remains the same.

November

The generally high temperature of the bottom waters over the whole area, resulting from the absence of cold water inflows, resulted in *C. proridens* penetrating as far as the extreme eastern part of the Bank (Fig. 3a); small fish dominated everywhere excepting inshore parts of the central zone, where different size groups occurred (Fig. 3b), and the north-western part (Fig. 4a). There was a notable increase of small, immature fish in the south-west of the Bank (Fig. 4b).

Of the overall patterns revealed by these investigations, it was clear that the large fish are associated with lower temperatures; they are most abundant in the eastern part of the Bank, which is affected by the cold water inflows, and penetrate into the western part only during periods of minimum bottom temperatures. Conversely, small fish are associated with higher temperatures, being in greater numbers in the western part and at the edge of the shallow plateau, extending to the east only when bottom temperatures are at maximum values.

One important point to emerge was the bimodal nature of the size distribution curves, the smaller size mode usually dominating (Figs. 3 and 4). Regarding mature fish, it was clear that the left part of the curve pertained to females; the right, to many fewer males. In virtually every case the difference in mean length between males and females proved highly significant statistically, indicating sexual dimorphism of the population as a whole (Fig. 5).

4. REPRODUCTION PATTERNS, LOCATIONS AND PERIODS

It was difficult to determine male maturity stages; thus ovary developmental stages only were used. During the study period more than 600 females were investigated from different parts of the shallow plateau; the great majority proved to be ripe and in a characteristic pre-spawning condition. However, as was verified by histological examination, never more than half the ovaries had eggs in this condition. Recent investigations of some demersal fish from lower latitudes have shown that partial spawning, as in *C. proridens*, occurs in many variations (Dekhnik *et al.*, 1970; Dimitrova, 1970; Domanevsky and Stepkina, 1971; Kulikova and Fandeeva, 1975; Morozov and Oven, 1968; Oven, 1961, 1965, 1967a, 1973, 1974; Oven and Salekhova, 1970; Salekhova, 1973; Talikina and Vorobyeva, 1975), and that specific variations in gonad development do not permit a generally applicable maturity scale suitable for use under field conditions (Koshelev, 1966; Naumov, 1974). The maturity stages used here are as follows:

III	Bulk of ovary consists of visually easily distinguishable, opaque oocytes of varying size (Ripening)
III-IV	Large, transparent oocytes visible among opaque oocytes of varying size (Ripening)
IV	Numerous large, transparent oocytes occupying, visually, about 20% of total volume of ovary (Pre-spawning)
VI-II	Absence of visually distinguishable oocytes; Ovaries limp and flabby (Spent)
II-III	Visually distinguishable oocytes absent or just appearing, ovaries resilient (Recovering or developing)

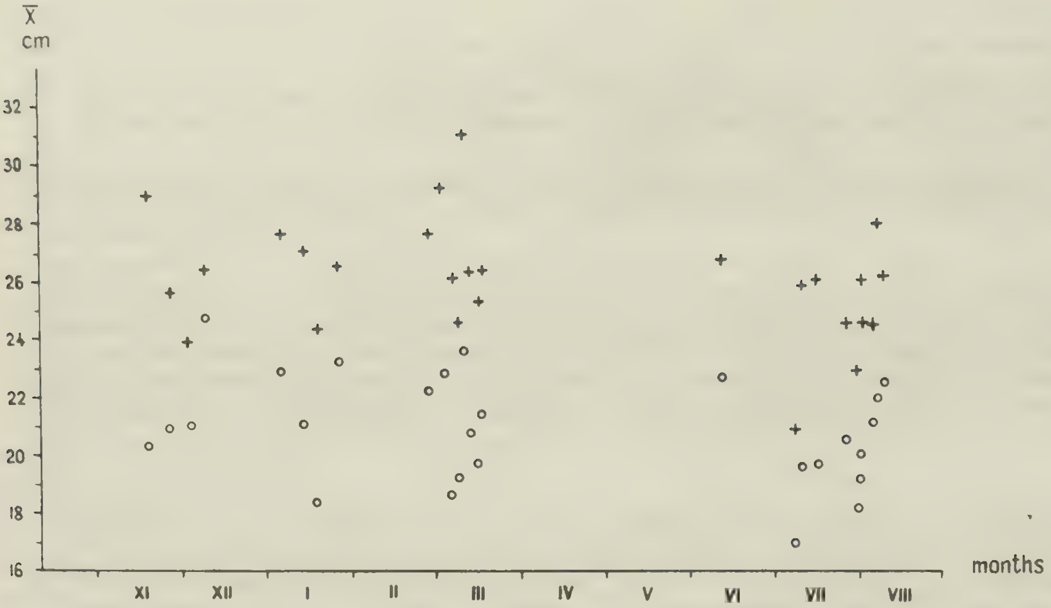
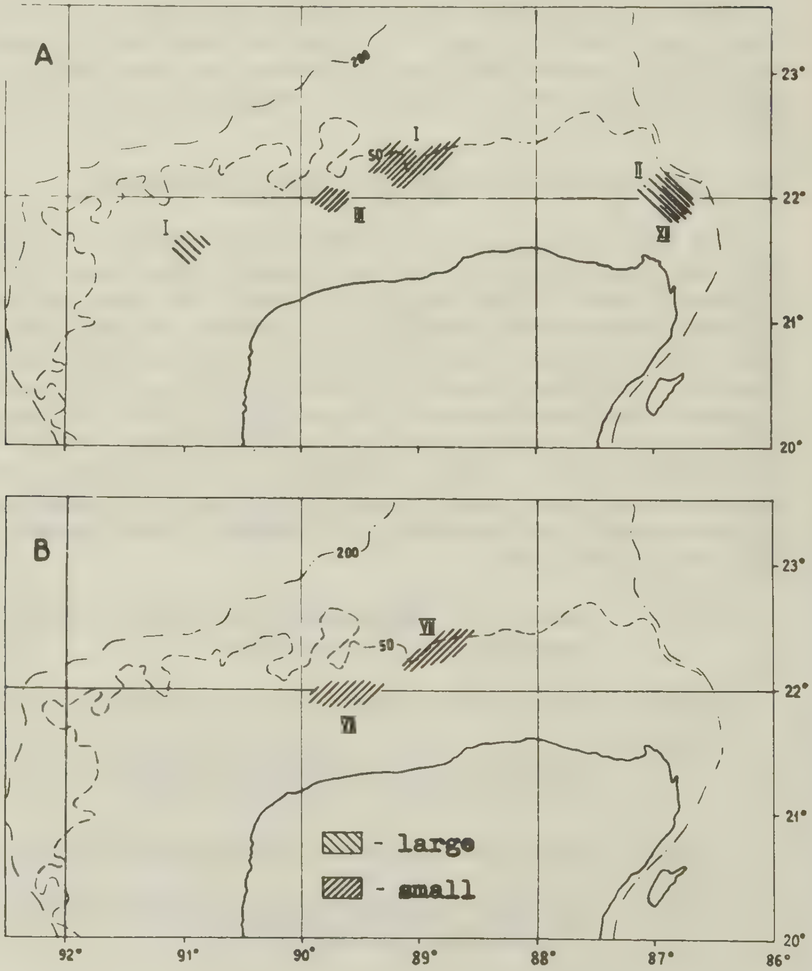


Fig. 5 Mean values of length of C. proridens females (circles) and males (crosses) for different months. (Overall mean length of females = 20.9 cm, of males = 26.6 cm)


A
200
I
50
II
III
XI
I
23°
22°
21°
20°
B
200
VII
50
VII
23°
22°
21°
20°
▧ - large
▨ - small
92°
91°
90°
89°
88°
87°
86°

A – December to March

B – May to August

Fig. 6 Locations and months of catching pre-spawning C. proridens on Campeche Bank. Roman numerals indicate the month

In accordance with the above stages, all specimens analysed fall into two groups, those with undeveloped ovaries and those with developed ovaries.[1] Only fish at stage IV were considered to be pre-spawning; stage V, i.e., the running ripe stage, was not observed, probably because of its very short duration.

The areas and times at which pre-spawning specimens were taken are shown in Fig. 6, with the size distribution shown as the shaded area in Figs. 3 and 4. Large, ripe specimens occurred from December to June, but the greatest abundance was in December and February, in the eastern part of the shallow area, and in January, in the western part of the shallow area, at the edge of the shallow plateau >35 m.

Pre-spawning small fish were observed from January to August, with peaks in January, March and July. As with the large fish, ripe small fish were observed in offshore areas >40-50 m, and only in the central area of the actual Bank (Fig. 6).

Over the spawning period a gradual size diminution of the fish actually spawning was noted. Thus, at the end of May and beginning of June, spawning fish were 22 cm long, in the first part of June 20 cm, in the second part 18 cm and at the beginning of August 17 cm. The end of the spawning period was dominated by small fish. At this period, asymmetry of the ovaries was often noted, the left being the larger.

As a general conclusion, C. proridens spawns from December to August and, although there is variation in numbers of pre-spawning individuals among fish of different sizes in different parts of the Bank, it is considered that peak spawning intensity is from January to March since it is during this period that the greatest number of pre-spawning specimens occurs and there is a lack of the post-spawning stages.

In common with some fish of temperate latitudes, C. proridens has sequential spawning of different size groups, and there are different locations of spawning grounds for different size groups, both of these factors no doubt being responsible for the lack of dense spawning aggregations.

From the data there can be little doubt that spawning of C. proridens is temperature-dependent although spawning intensity is variable (Fig. 7). Onset of spawning is coincident with the appearance of cold water inflows into the eastern part of the shallow plateau during December, this apparently stimulating the large fish to commence the spawning cycle. It would appear that plankton development is also temperature-dependent, maximum biomass figures being noted from January to August (Jrómov, 1967). Plankton is maximal therefore during the early developmental stage of C. proridens.

5. SEASONAL CHANGES IN FAT CONTENT AND FEEDING INTENSITY

Intestinal or body cavity fat content in mature fish varies considerably over a year, conforming to a regular pattern. Maximum accumulation is in November-December, coinciding with the onset of spawning. Over the reproductive period the fat deposits decrease, due no doubt to their utilization in sexual product development, generally disappearing by the termination of spawning. However, in July and August there begins a rapid build-up of fat in large post-spawning fish.

This general pattern is the same in fish of different size groups but the monthly mean values of fat content are usually lower for small fish and the fluctuations smaller (Fig. 8 and Table III). It should be noted that during the period of spawning, irrespective of size the fat content is higher in fish living in deeper water; i.e., near to spawning grounds (Fig. 8).

---

[1] Stages III, III-IV, IV are characterized by developed sexual products
Stages VI-II, II-III are characterized by undeveloped sexual products

TABLE III

Intestinal fat content of females in different maturity stages
by month during the sampling period 1969–71
(Where two figures or sets of figures appear above and below a line,
the upper figures refer to fish <20 cm and the lower figure to fish >20 cm)

Maturity Stage	Monthly mean values of intestinal fat content									
	November	December	January	February	March	April	May	June	July	August
II-III	1.0–1.4	$\frac{0.3}{0.9}$	–	–	–	–	–	0.2	1.0–1.5	0.2–1.7
III	$\frac{1.0-1.4}{0.9-1.7}$	$\frac{0.9-1.4}{1.1-1.7}$	0.4–0.7	0.2	0.1–0.9	–	–	0	0.2	–
III-IV	–	–	0.7	0.2	0.1–0.2	–	–	0	0.0–0.2	0.1–0.9
IV	–	–	0.7	0.4	–	–	–	–	0.4	–

Over the year feeding intensity is variable (Fig. 9). The main feeding grounds of mature fish are the inshore parts of the plateau and feeding is, generally, concentrated around the spawning and post-spawning periods. At the edge of the plateau, nearer the spawning grounds, intense feeding was noted only before spawning, it being negligible at other times. As would be expected, there is a relationship between intestinal fat and feeding intensity (cf. Figs. 8 and 9).

Tooth structure in C. proridens, with the presence of grinding teeth, can be associated with feeding on animals having hard covers, i.e., relatively inactive benthic animals such as crabs and bivalves. However, to the west of the area, south of 20°N, the main food of young fish is Penaeus duorarum.

6. CONCLUSIONS

The overall picture of the biology of C. proridens is as follows. It is clear that all stages of the life cycle occur in the shallow waters of the Yucatan Peninsula (Fig. 10). Spawning occurs in various parts of Campeche Bank between 87°W and 91°W at the edge of the plateau at a depth of 35–55 m. Irrespective of the precise location of the spawning grounds there is a steady drift westward of the pelagic eggs and larvae, these latter eventually reaching a shallow zone, where the demersal habitat is adopted. For the first year the fingerlings remain in the inshore waters, which are relatively richer in food; growth at this stage is rapid. Between the ages of one and two there is a gradual movement off-shore toward the north-east and east, where the small fish recruit to the commercial stock.

Females 18–22 cm long predominate in the mature fish stocks. There are strongly developed migration patterns in these mature fish during the period of reproduction. The general pattern is a movement toward the edge of the shallow plateau, limited by a depth of 50 m, a partial spawning there, a movement back inshore with intensive feeding, the so-called "interspawning" period, and then another outward movement and further spawning until the fish are spent. This series of partial spawnings extends over about eight months although, within this period, the intensity varies. Peak spawning for large fish is January – March, on the eastern and north-western spawning grounds, and for the small fish, which constitute the bulk of mature population, in January, May and July in the central part of the Bank. The extended spawning period is reflected in the considerable differences both in length and weight within any year class and the different times at which corresponding periods within the annual cycle are reached.

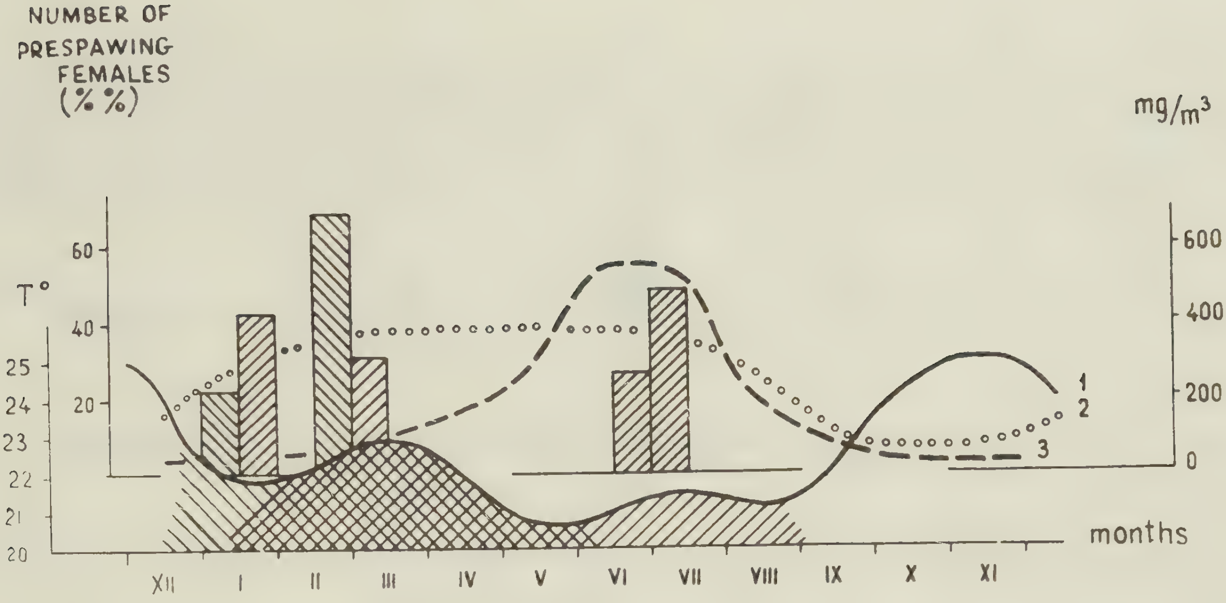


Fig. 7 Reproductive period of C. proridens and related factors on Campeche Bank. 1 - bottom temperatures, 1969-71; 2 + 3 - total plankton biomass. Note: the mean plankton biomass values between the 20 m and 200 m isobaths have been calculated for 91°W (2) and 87°20'W (3) from N.S. Jrómov (1967, Fig.5)

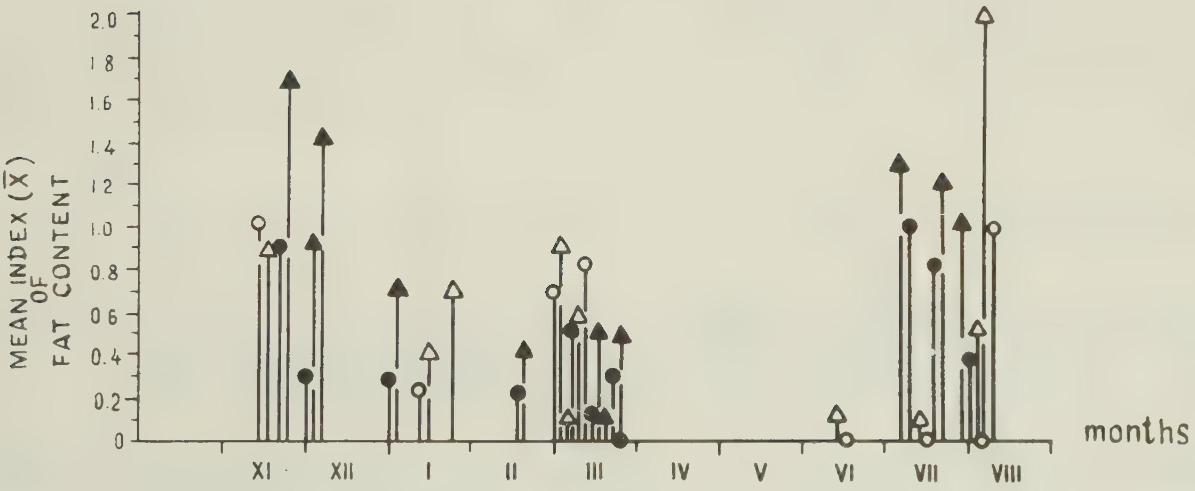


Fig. 8 Seasonal changes in fat content of mature C. proridens. Circles represent small specimens; triangles represent large specimens. Solid symbols refer to depths >30-35 m; open symbols to depths <30-35 m

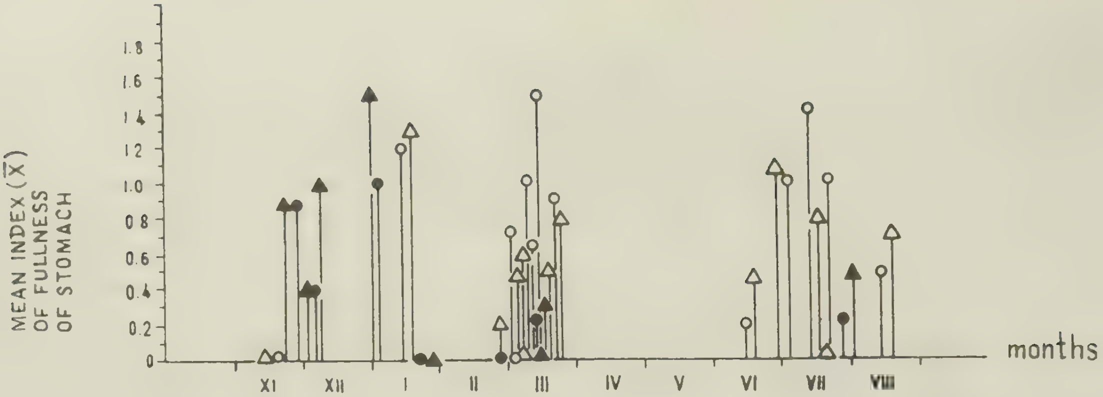


Fig. 9 Feeding intensity of small mature and large mature specimens of C. proridens by month. Symbols as in Fig. 8

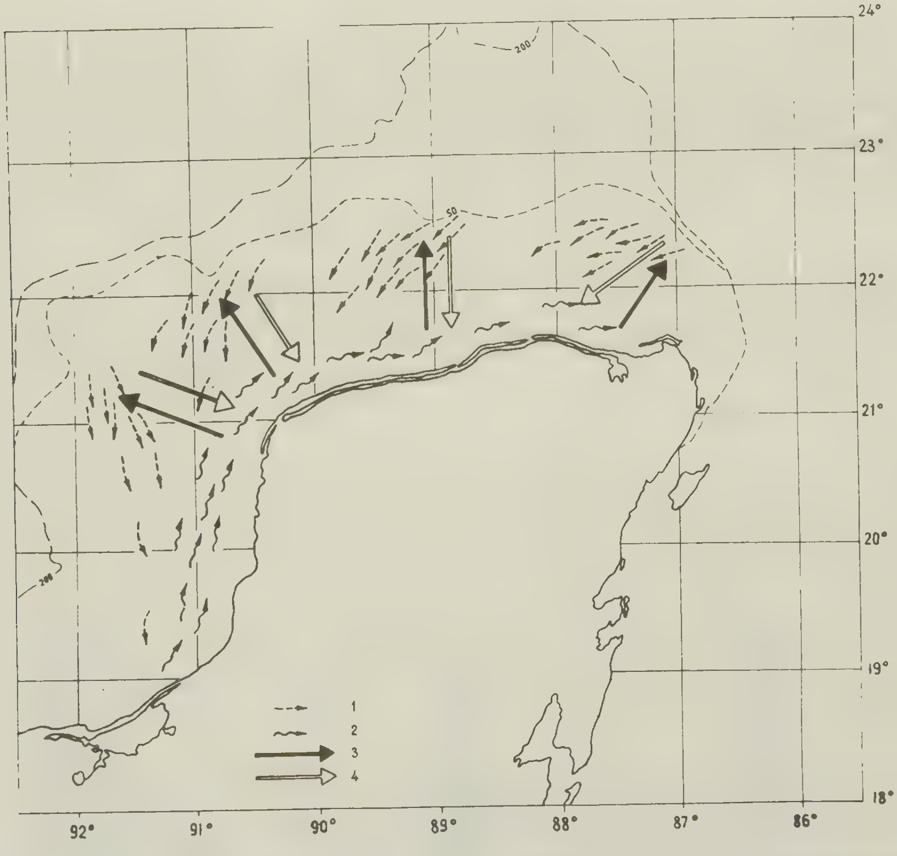

24°
23°
22°
21°
20°
19°
18°
200
50
200
1
2
3
4
92°
91°
90°
89°
88°
87°
86°

Fig. 10 Schematic representation of migrations of C. proridens on Campeche Bank.
1 – drift of eggs and larvae; 2 – migrations of immature specimens;
3 – spawning migrations; 4 – post-spawning and feeding migrations

These differences appear clearly in Table IV, which for selected months shows the variation in the observed incremental growth of scales since formation of the outermost ring, expressed as a fraction of the width of the zone between the outermost and previous rings. Evidently there is substantial variation in the timing of growth, spawning or ring formation, probably related to differences in the annual cycle of activities among fish of different size groups.

TABLE IV

Variations in scale increments during the last year of life (Data of 1969-71)

Months	Relative frequency (%) of fish with:				Number of fish sampled
	Increment less than 1/3 of the previous annual one	Increment 1/3-1/2 of the previous annual one	Increment more than 1/2 of the previous annual one	Negligible increment	
July	30.1	18.7	19.5	31.7	125
November-December	20.2	15.3	1.5	63.0	65
January	32.0	22.0	2.0	44.0	50
February-March	40.0	28.3	6.7	25.0	60

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SPAWNING PATTERNS OF FISH FROM THE NORTHEASTERN CARIBBEAN

by

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CONTENTS

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2. METHODS
3. CODE SYMBOLS USED
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Abstract

Precise life histories of most fish species are still unknown. Twenty-three years of continuous observations on seasonality of gonad ripeness, presence of leptocephali, post-larvae and juveniles are combined with relevant data from the literature and charted for 350 marine and fresh water fishes from this region.

Individuals of many marine species were found to spawn year-round with seasonal peak spawning once or twice during the year in some cases. Fewer species showed limited and well defined spawning periods. Further evidence of periodic spawning was the frequent occurrence of gonads found in repose in adult fishes.

In some species fat bodies attached to the gonads indicated an approaching spawning period.

Resumen

No se conocen aún con exactitud los ciclos vitales de la mayoría de las especies de peces. En este trabajo, utilizando los datos obtenidos en observaciones continuas hechas a lo largo de 23 años sobre la periodicadad de la maduración de las gónadas y la presencia de leptocephali, formas post-larvales y formas juveniles combinándolos con datos procedentes de otros estudios, se ha preparado una serie de tablas sobre 350 peces marinos y de agua dulce de la región.

Se ha hallado que en muchas especies marinas hay individuos que desovan a lo largo de todo el año, con puntas máximas estacionales una o dos veces al año en algunos casos. Las especies con períodos de desove limitados y bien definidos son menos. Otra prueba de la periodicidad del desove es la frecuente presencia de gónadas en estado de reposo en peces adultos.

En algunas especies, la presencia de cuerpos grasos adheridos a las gónadas indica que se aproxima la temporada de desove.

1. INTRODUCTION

Phenology, the timing of critical events in the life history of animals, has been a lifelong interest with me and, early it became concentrated on fish and sea life. Although the question "when does a fish spawn?" appears at first simple, the longer one studies it the more variations arise, areas differ, years differ, so that one becomes more, rather than less, hesitant to state rules.

Indications of seasonal, periodic, or intermittent spawning are recorded in this paper for 350 species of fish, 336 salt water and 14 fresh water. Most of the specimens were observed from around Puerto Rico, where I have been engaged since 1954 in fresh and salt water sport fish restoration programmes, and in studies of commercial fish for the Puerto Rican Department of Agriculture. A few data stem from earlier visits.

Relevant information was acquired on several offshore cruises; thus the region included in the paper extends from Antigua (17°N and 62°W) northwestward to Silver Bank (21°N and 70°W) and includes the Virgin Islands. Items from the literature have been added to round out the picture to date.

2. METHODS

The incontrovertible proof of spawning periods is, of course, the recurring presence of ripe ova and testes in numbers of individual fishes. Weekly, if not daily, during my years in Puerto Rico I dissected fish as they came in from sport or commercial fishing to determine gonad ripeness and stomach contents. Coded in the chart are data for those fishes which were either stage III - sub-ripe gonads, or stage IV - ripe gonads. Complementary data, equally important, were obtained by observation of the times and numbers of fish when they were not near spawning condition, when gonads were recessed, though these observations are not individually recorded in this paper.

Indications of recent spawning periods were gained through observation of the presence and relative abundance of post-larval fish, both reef and pelagic species. These post-larval fish I discovered by means of stomach content studies and collections dip-netted under night-lights. I carried on frequent dip-netting chiefly at La Parguera, near the southwest corner of Puerto Rico, from 1954 to 1966. Periodic dip-net collections at river mouths provided data on post-larval fish migrations up the rivers from the sea.

The American Museum of Natural History prepared gonad sections of serranids and blue marlin (*Makaira nigricans*) for microscopic study, and the Florida Department of Natural Resources, bonefish (*Albula vulpes*).

The appended list entitled "Seasonal spawning indications for fishes from the N.E. Caribbean" is in phylogenetic order following Greenwood *et al.* (1966).

3. CODE SYMBOLS USED

el = few elvers; EL = large numbers of elvers; em = embryos in early stages, as in sharks, rays or other fishes; EM = embryos in terminal stages of development; EP = fertilized eggs in pouches of male sygnathids; f = ovaries with sub-ripe ova, usually yellow or opaque white, and clearly distinguishable without magnification. Most developed ovaries are stage III; F = ovaries with ripe ova, usually transparent and colourless, stage IV; j = juvenile fish; J = great concentrations of juveniles; le = leptocephali; LE = seasonal peak numbers of leptocephali; m = sub-ripe enlarged testes with slight or no loose milt, stage III; M = ripe testes with loose or running milt, stage IV. Ripe testes are often smaller than stage III; nu = male nuptial colours; po = post-larvae; r = both males and females with sub-ripe enlarged gonads, stage III; R = both males and females with ripe gonads, stage IV; spr = spring, when it is not more precisely defined in the literature; yr = year round spawning, indicated mainly in the literature.

The number in parentheses following a fish name represents the actual, or approximate, number of individuals of the species examined. The numbers at the end of the line indicate references.

4. DISCUSSION

4.1 *Marine Fishes*

Unlike most northern fish, with their distinct spawning periods, tropical fish tended to show prolonged spawning periods. Individuals of some species were found in spawning condition any month of the year; other species showed peak periods in addition, when greater numbers of individuals were in spawning condition. Few species had limited spawning periods. During the first half of the year more species, in both marine and fresh waters, were found in spawning condition.

Sharks: Because of the long and uncertain periods of gestation, periodicity in shark spawning was inconclusive except, possibly, for two species. Recently born nurse sharks, *Ginglymostoma*, appeared in numbers in September 1956, 1957 and 1965. Local fishermen reported young nurse sharks in late summer. In September 1974 and 1975, small sharpnose sharks, *Rhizoprionodon*, still showing red umbilical scars, bit on handlines at night or were caught in gill-net sets in Bramadero Bay south of Mayaguez.

Bonefish: Numerous *Albula* leptocephali (423 measured from 44 to 66 mm S.L.) appeared under nightlights every month of the year at La Parguera, but larger numbers were observed from March to May. More ripe or sub-ripe adults were found in January than other months; 351 adults were dissected for gonad analyses. Enlarged fat bodies attached to the gonads preceded gonad development.

Elops leptocephali, 26-30 mm, were collected once, in September 1959, from the Añasco river mouth. *Megalops*, 24-28 mm, appeared at the same time. *Megalops* were also collected from the south of the Guanajibo River in July 1968 and September 1974.

Eels: *Anguilla rostrata* leptocephali, 78-96 mm, were collected at La Parguera in June 1962 and July 1964. Numerous elvers were reported at Dos Bocas dam on 17 November 1947. Over 100 elvers were collected from the Culebrinas River at Margarita dam on 5 December 1972.

Batfishes: *Ogcocephalus parvus* and *O. vespertilio* males displayed nuptial colouring, red lips and pinkish abdomen, during the spawning season from January to April.

Flying fish: *Cypselurus heterurus* (ripe adults) was the more common larger flying fish species found in dolphin (*Coryphaena*) stomachs from December to April (*Parexocoetus brachypterus* was the other), the time of profuse spawning and greater abundance of both species.

Houndfish: *Tylosurus crocodilus* juveniles were found in March off La Parguera, especially during calm spells, in conjunction with large floating beds of *Sargassum*, such as in late March 1959 and 1969. Masurekar (1968) described large bunches of eggs washed ashore along the coast of Bombay in October and November.

Silversides: *Allanetta harringtonensis* were observed one July afternoon in a large school, all ripe males and females, milling around, crowded in shallow water over sand bottom, actively spawning. They were slow and easily caught with a small seine. This was off the east coast of Puerto Rico at Lobos Cay, east of Fajardo. As common as are silversides, of the very few times I have seen them in spawning condition this was the most impressive.

Red hind: *Epinephelus guttatus* spawning runs took place one or two days after the full moon in January or early February off La Parguera from 1954 through 1966 except for 1957 and 1965, when there were no well defined runs. At other times of the year adult red hinds had undeveloped gonads.

Snappers: Lutjanidae spawned more in spring and summer. From March through May off San Juan, and over Silver Bank in early September, 80 percent of adult yellow-tail snappers, *Ocyurus chrysurus*, had ripe or sub-ripe gonads, whereas in November and December all those dissected had undeveloped gonads. The closely related lane snappers, *Lutjanus synagris*, spawned from March to September, with a peak in May, along the west coast south of Mayaguez. At La Parguera, one female with sub-ripe ovaries was found as early as 30 January.

Deep-water red snappers such as *Rhomboplites aurorubens*, *Lutjanus vivanus* and *L. buccanella* had varying spawning patterns. Off the south coast of Puerto Rico, 71 percent of 150 *Rhomboplites* had sub-ripe or ripe gonads in February and March 1976, and 87 percent of 143 from April to June. On the other hand, in that same period, 25 percent of *L. buccanella* had gonads approaching spawning condition, and only three males of 141 *L. vivanus* had slight amounts of milt in small testes. In March 1969, at offshore Grappler Bank, of 24 silk snapper adults, there were four males with ripe testes and five females with sub-ripe stage III ovaries, and at Anguilla Bank in April 1968 there were 11 stage IV males and 16 stage III females among 46 silk snappers. There may be less spawning close to the coast compared with offshore areas.

Grunts: Pomadasyidae did not show well defined spawning periods. Individuals of *Conodon nobilis* were found in or near spawning condition in all months except March-April and June-August in the same habitat south of Mayaguez as the lane snapper.

Jacks (Carangidae): Post-larval blue runners, *Caranx crysos* (Mitchill), or *C. fusus* (Geoffrey-St. Hilaire), a possible synonym, occurred in 4 percent of 600 dolphin stomachs. These post-larvae averaged 50 mm and were more frequent and numerous in dolphin stomachs during April-May than other months.

Several large runs of juvenile blue runners were reported at La Parguera from September to November 1956. On 4 October, a boat caught 97 blue runners averaging 200 mm in length and weighing 12.7 kg. On 2 November, two seine hauls produced 100 kg of blue runners of similar size. Such numbers of blue runners were not seen again other years through 1965. Even the size class was rare. Local fishermen believed these unusual runs of small blue runners were caused by disturbed weather. A small hurricane had passed through the eastern part of the island on 12 August 1956.

A few adult blue runners, 500 g or more in weight, were caught by the La Parguera fishery every year. More of these adult blue runners were in spawning condition from March through May than at other times of the year. The spawning for the species, however, is protracted.

The ubiquitous leatherjacket, *Oligoplites saurus*, has a habit of jumping out of water. In March, April and November, running ripe females jumped out and landed in my boat, incidentally demonstrating protracted spawning for the species. Other jacks with prolonged spawning periods were *Caranx latus*, *C. ruber*, *C. hippos* and *C. lugubris*.

Dolphin: Of 600 *Coryphaena hippurus* dissected, 90 percent of adult females had stage III sub-ripe ovaries throughout the year except for August, when no dolphins were examined. The largest and smallest females with stage III ovaries were a 41 pounder (19 kg) in February and a four pounder (2 kg) in July. Greatest numbers of dolphin were caught in February, when greater spawning activity was indicated by the presence of more semi-transparent ova in the ovaries. Females outnumbered males three to one.

In dolphin stomachs, I found 51 species of post-larval or juvenile fishes. Only flying fish were usually adults. There were changes in the diet of dolphins which reflected the seasonal availability of fish species near the sea surface. Seasonally the chief species found in dolphin stomachs were:

Winter = *Cypselurus heterurus*, *Hemiramphus balao*, *Acanthurus* spp., *Cantherines pullus*;

Spring = *Parexocoetus brachypterus*, *Cantherines pullus*, *Psenes cyanophrys*, *Caranx crysos*;

Summer = *Cantherines pullus*, *Balistes capriscus*, *Priacanthus* spp.;

Autumn = *Xanthichthys ringens*, *Cantherines pullus*, *Pseudupeneus maculatus*.

The most numerous and frequent year-round food animal of dolphin and other pelagic fishes was the juvenile filefish, *Cantherines pullus*, averaging 50 mm T.L. Remarkably abundant in late September and October were sargassum triggerfishes, *Xanthichthys ringens*, 50 to 75 mm.

Porgies: Sparidae had a limited spawning season. At La Parguera on 16 February 1954, over 100 *Archosargus rhomboidalis* crowded into one fish pot in less than two fathoms of water. Most were females, 200 to 220 mm S.L., with running ripe transparent ova. In following years, February continued to be the peak spawning month of this species, although spawning extended from November to March. *Calamus pennatula* and *C. penna* were found in spawning condition in February and March.

Mullets: Most Mugilidae showed concentrated spawning in autumn and winter. *Mugil liza* is known to be heavy with spawn in January. At the end of a spawning run in mid-December in a mangrove lagoon at Joyuda, on the west coast of Puerto Rico, of twelve *M. curema*, 245 to 354 mm F.L., seven were sub-ripe, five females and two males. The bodies of these mullets with developed gonads were elongate, similar to river fish. The five mullets with short, deep bodies were like sea-run mullet and contained undeveloped gonads. Juvenile *M. curema*, 25 mm, were present all months off La Parguera, more numerous in February.

Agonostomus, unlike the other mullets, were found ripening in June in the fresh waters of Melania Reservoir; sub-ripe females and a ripe male. Post-larvae were dip-netted at sea under lights at night off Aguadilla, in October.

Joturus pichardi, the hog nose mullet, according to Cházari (1884) who quoted Mexican fishermen, spawned at river mouths in October; the adults returned upstream in November and the young migrated upriver in December. *Joturus* occurs in the Añasco River (Erdman, 1974).

Barracuda: *Sphyraena barracuda* juveniles of 25 mm were found every month in the year off La Parguera, though they were more numerous in summer and autumn. Few adult barracuda contained ripe gonads in winter. Enlarging fat bodies preceded the ripe gonads.

Parrotfish: Scarids are commonly associated with coral reefs and form a large portion of the fish-pot catch. Of the many parrotfish from the commercial catch dissected, most had completely recessed gonads; only a few were developed or ripe, and yet juveniles were present all year. On two occasions in December 1956 when I observed several ripe fish, the transparent, flowing ova of *Sparisoma aurofrenatum* were round, and those of *Scarus taeniopterus*, elongate, a noteworthy difference described by Winn and Bardach (1960).

Gobies: Three species of Gobiidae exhibited male nuptial colours from May to November. *Sicydium plumieri* spawned in the fast upland streams on rock or rubble bottom, and post-larval migrations upriver from the sea began at river mouths at, or just after, the last quarter phase of the moon from July through December (Erdman, 1961). *Evorthodus lyricus* males sported two red stripes on a long tail and red on the anal fin in May at the Guanajibo River mouth, and in August at the Sabana River. *Gobionellus boleosoma* males, in a mangrove lagoon near Luquillo beach in November, displayed a broad red stripe on the upper edge of the tail and a small red band near the edge of the pectoral fin. An eleotrid goby male, *Gobiomorus dormitor*, 356 mm, from Loiza reservoir in August, showed dark green nuptial colour.

Blennies: *Hypleurochilus aequipinnis*, the oyster blenny in December was observed protecting its eggs in an open oyster shell on a mangrove root in a shallow, mud bottom bay east of La Parguera. The terminal embryos were wiggling actively and their hearts beating rapidly. Another oyster blenny in December and one in March were seen guarding less developed eggs in oyster shells.

Tuna: Scombrids carried on prolonged spawning. *Euthynnus pelamis* individuals were found in, or near, spawning condition (stage III or IV) every month of the year. *Scomberomorus cavalla* were in spawning condition mainly in July and August, but I found one female with translucent ova as early as 10 April and a ripe male as late as 12 November. *S. regalis* showed less peaked and more extended spawning, virtually all year. *Thunnus atlanticus* juveniles, 250 mm, formed the bulk of stomach contents of blue marlin in September. More ripe adults were found in April-May and September-October, the clearest example of bimodal peaks which I encountered. Two bluefin tuna, *T. thynnus*, a female 305 lb and a male 261 lb, with gonads in repose, were caught off San Juan on 18 January 1960.

Blue marlin: Of a total of 633 *Makaira nigricans* dissected for gonad studies, 485 were males and 148 females. Some 400 of the males were approaching or in spawning condition from May through November. During the 23 years of my study, however, there were only three females with transparent running ripe ova: 24 September 1966, 246 lb (Erdman, 1968), 6 September 1970, 276 lb and 12 September 1975, 282 lb. All three were thin and in poor condition; undoubtedly they were partly spawned out. Females were more frequently caught in July and August, when sex ratios were nearly equal. Two post-larval blue marlin were caught in a neuston net 60 miles south of St. Croix on 9 November 1972 (DISCOVERER cruise, CICAR programme).

Triggerfish: *Balistes capriscus* juveniles from 25 to 40 mm were frequently found in pelagic fish stomachs, but the adults were rarely caught in fish-pots. *B. vetula*, on the other hand, is commonly caught thus; juveniles are rare in collections. In February, at Mona Island, I observed two 45 mm *B. vetula* which could swim only downward at a 45° angle, probably a temporary adaptation from post-larval planktonic life to the juvenile and adult bottom existence.

4.2 Fresh Water Fish

More than 20 species of exotic fresh water fish are established in Puerto Rico and reproduce in the wild. My observations indicated that North American species tended to have longer spawning periods here than on the continent.

Threadfin shad: Forty ripe *Dorosoma petenense*, 100 mm F.L., were stocked in Guajataca reservoir on 30 May 1963. Evidence of reproduction appeared a year later, 9 June 1964, when two size groups were caught, 40 post-larvae, 10-19 mm in length, and eight juveniles, 21-28 mm. Since then shad have been abundant in this 800 acre reservoir.

Catfish: The four species of *Ictalurus* in the reservoirs were found with developed ovaries and ova from January to March.

Rosy barb: Nuptial coloured males of *Barbus conchonius*, with females, were seined from Rio Arroyata in late March 1971 and transferred to the Maricao Fish Hatchery, where the first successful spawning took place the following year in early May.

Bass: Largemouth bass, *Micropterus salmoides*, peak spawning was in the cooler weather at both Maricao, in the mountains, and the reservoirs nearer sea level, from January to March. Individual pairs at Maricao have spawned at the end of December and, on one occasion, a pair spawned in August. *M. coosae* spawned in the rivers mainly in March and April.

Sunfish: The bluegill sunfish, *Lepomis macrochirus*, was introduced to Puerto Rico in 1915. At Maricao, and in the wild, they have spawned year-round. Evidence of lunar-related activity occurred when a large group of small bluegills spawned profusely at Patillas reservoir during the fifth and sixth day after the full moon in July 1964.

The other sunfish, the shellcracker, *L. microlophus*, and the redbreast, *L. auritus*, showed more restricted spawning periods. Nuptial black male shellcrackers were seen guarding their nests in shallow water at Loiza and Dos Bocas reservoirs in February and March. Their spawning was observed to follow the full moon at the same interval as the bluegills. A few redbreast males were seen in March guarding nests on sand bottom downstream from Jayuya.

Tucunaré: Cichla ocellaris fingerlings, 60 to 80 mm, were received from the Buga fish hatchery, Colombia, on 27 January 1967. The first hatch of fry at Maricao occurred six months later on 8 August. Thereafter, successful spawning at Maricao took place only from May to August because of low water temperatures the rest of the year. To hatch eggs successfully, tucunaré required water temperatures of 27°C or above. Increasing information on tucunaré in the reservoirs has indicated more extended seasonal spawning. A male with a nuptial red nuchal hump, characteristic of the spawning period, was caught in Las Curias reservoir on 18 October 1972: it weighed 800 g and measured 380 mm. Two adults accompanying 25 mm fry were reported at Toa Vaca reservoir on 25 January 1974. In spite of these incidents of late season and winter spawning, more profuse spawning occurred during the spring and summer.

Tilapia: Tilapia mossambica, T. hornorum and T. melanopleura rendalli spawned year-round, with somewhat lessened activity in winter.

5. SUMMARY

Individuals of most fish species considered here were found in spawning condition any month. It was also true that individual adults of most species had gonads in repose, or completely resorbed, any time in the year. Post-larvae of several species were found in all months.

Year-round presence of post-larval reef fish in various pelagic fish stomachs indicated prolonged spawning of squirrelfish, goatfish, doctorfish, trigger and filefish.

Year-round presence of juveniles indicated intermittent spawning of coral reef fish such as pomacentrids, labrids and scarids, with slight seasonal variation. Common and numerous as adult scarids were, they were almost always found with resorbed gonads.

Many fish, such as bonefish, spawned year-round, with one or more periods of intensified spawning. Moon phase correlated with peak spawning of a few species such as the fresh water gobies.

Pelagic fish, dolphin and skipjack tuna, were found with near-ripe ovaries throughout the year; blue marlin had developed gonads, or ripe gonads, between late March and early November.

Fish in the same family tended to have similar spawning patterns. Sparids spawned in winter, lutjanids in spring and summer and carangids year-round.

Certain fish species in spawning condition, red hinds and yellowtail snappers for example, were easier to catch than the same species with undeveloped gonads, a fact recognized by commercial fishermen.

Introduced fresh water fish from temperate zones, largemouth bass and bluegills, showed more protracted spawning in Puerto Rico than in their native habitat.

In a number of species, ripe males were found both earlier and later than ripe females.

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SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references	
1			R	R			Asymmetron lucayanum	1
2			em				Rhincodon typus (1)	2
3				em	em	em em	Ginglymostoma cirratum (10)	3
4					em	em	Galeocerdo cuvieri (2)	3
5	em		j,m				Negaprion brevirostris (3)	4
6	j,em	F j		em	j j	j j,em	Rhizoprionodon porosus (24)	5,6
7		spr	spr				Carcharhinus acronotus (4)	7
8		EM		em			C. falciformis (10)	8
9	em	EM	M M	M	em	em em	C. limbatus (10)	7,9
10	em	em EM					C. longimanus (10)	10
11			j				C. maculipinnis (1)	
12			em				C. springeri (10)	6
13	EM				em	m	Prionace glauca (1)	11,12
14		EM					Mustelus norrisi (10)	
15		em f		EM		EM j	Sphyrna mokarran (10)	3,13
16		em			EM em		Dasyatis americana (3)	3,6
17				EM		em	Aetobatus narinari (10)	14,15
18		em					Manta birostris (1)	14
19	f,	M,f f			le	f, f	Elops saurus (20)	3,16,17
20	f		j,m	le	le		Megalops atlantica (18)	5,16,17
21	R R	LE	LE	le	le M	le	Albula vulpes (351)	19,20
22	EL		le	le	el	EL EL	Anguilla rostrata (200)	21
23	f						Conger triporiceps (1)	
24	le			le	le		Rabula acuta	22
25		f					Gymnothorax funebris (10)	
26	F	f					G. moringa (10)	6
27		f				f	G. vicinus (10)	6

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references	
28		F			j		Echidna catenata(2)	23
29		spr					Muraenesox savanna (1)	5
30		f					Ophichthus gomesi (10)	
31					f		O. spinicauda (1)	
32					po		Synaphobranchus infernalis (10)	
33		R	R	R			Moringua edwardsi	24, 25
34	le	EL				le	Myrophis punctatus	26
35	r	F f	F r				Harengula humeralis (200)	27, 28
36			F				H. pensacolae (200)	27, 29
37		f	M R	r			Opisthonema oglinum (500)	30
38	f f						Jenkinsia lamprotaenia (200)	5, 31
39	R R						Sardinella anchovia	32, 33
40				F			Anchoa hepsetus (1)	
41		r					A. lyolepis (50)	
42	r						A. parva (100)	
43	f		f				Cetengraulis edentulus (50)	34
44					f		Chirocentrodon taeniatus (4)	
45	m	f f,M				PO M	Synodus intermedius (100)	6, 35
46	yr	yr	yr	yr	yr	yr	Acyrtops beryllinus	36
47			R	R,j			Gobiesox strumosus	37
48		f					Acyrtus rubiginosus	38
49	yr	yr	yr	yr	yr	yr	Histrio histrio	39
50	nu						Ogcocephalus parvus (1)	40
51	nu	nu					O. vespertilio (10)	
52		f					Brotula barbata (1)	
53			em				Ogilbia cayorum (1)	
54	R F	f f,F				f M,f	Cypselurus heterurus (200)	

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references	
55				R			C. cyanopterus (1)	41
56	R R						C. comatus (1)	42
57	f		R		R R	R R	Parexocoetus brachypterus (100)	43
58	yr	yr	yr	yr	yr	yr	Exocoetus volitans (2)	42, 44
59	j						E. obtusirostris (1)	
60	F			F			Hirundichthys speculiger	42
61	yr	yr	yr	yr	yr	yr	H. affinis (2)	45
62		F					Prognichthys gibbifrons (6)	
63		F		F		F	Oxyporhamphus micropterus	42
64		F					Euleptorhamphus viridis (10)	
65	f	F F					Hemiramphus brasiliensis (300)	
66	f	f					H. balao (50)	
67		f					Hyporhamphus unifasciatus (1)	5
68	f						Chriodorus atherinoides (1)	1
69		f	F				Strongylura timucu (1)	6
70			F				Platybelone argalus (10)	
71		j,f			F	F	Tylosurus crocodilus (20)	5, 46
72			f f	F			Atherinomorus stipes (200)	
73			r	R			Allanetta harringtonensis (1000)	
74				F			Melanorhinus microps (5)	
75	R	m			R		Holocentrus ascensionis (150)	35
76	R	f,M	R	M	R M		H. rufus (122)	35
77	f						H. marianus (4)	
78	j	j	j		j	j	Ostichthys trachypomus (20)	
79		po	po	po	po	po	Holocentrus vexillarius (10)	47
80		f					Myripristis jacobus (7)	
81	F	j j	j	j	j	f,j	Aulostomus maculatus (12)	35

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references
82				j			Fistularia tabacaria (5)
83	Ep	Ep		Ep			Syngnathus dunckeri 1
84	Ep	Ep		Ep			S. elucens (1) 1, 48
85	Ep						S. jonesi 48
86				Ep			S. pelagicus 1
87	Ep Ep						S. rousseau 5, 6
88				Ep Ep			Corythoichthys brachycephalus (10) 49
89	Ep						C. albirostris (1) 1
90		Ep		Ep	Ep		Oostethus lineatus (10)
91		Ep	Ep	Ep			Hippocampus reidi (2) 50
92				R			Scorpaena bergii 27
93						j	S. grandicornis (5)
94				j			S. plumieri (20) 28
95				F			S. brasiliensis 6
96	j	j M	j	j	j		Dactylopterus volitans (40) 28, 51
97	f	f R	F	j	M		Centropomus undecimalis (20) 5, 18
98	f	f f					C. parallelus (24)
99		f	f			j	C. ensiferus (20) 5
100		R	R	R			Epinephelus cruentatus (9) 35, 52, 53
101	f			F		f	E. fulvus (146) 35
102				R R	j		E. itajara (14) 54
103		F					E. flavolimbatus 55
104	po	M j				f	E. striatus (32)
105	R R						E. guttatus (144)
106						f	E. adscensionis (10)
107	f	f R	R				E. morio (37) 56
108	f	F		F		F	E. mystacinus (64) 35

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references	
109					F		E. inermis (7)	6
110	f					f,M M	E. afer (10)	48
111	M,f	M,f M	R				Mycteroperca venenosa (41)	35
112	M	f					M. tigris (10)	40
113	j						M. interstitialis (11)	
114	j	f j,f					Paranthias furcifer (10)	5
115		F					Diplectrum radiale (10)	
116	f	F					Serranus phoebe (10)	
117		spr					S. tabacarius (10)	5
118		r,R					S. tigrinus	28
119				R			S. tortugarum	27
120		R					Bullisichthys caribbaeus (1)	57
121		spr					Dules dispilurus	5
122		R					Gramma loreto	58
123				R	R		Pseudopriacanthus altus	59
124		f					Priacanthus cruentatus (10)	
125			r		F	f	P. arenatus (10)	
126			em	F			Apogon maculatus	27
127		f					A. binotatus	5
128			em	em			A. pseudomaculatus	14
129	f						A. pigmentarius	5
130			em		em		Astrapogon stellatus (10)	1
131		m					Malacanthus plumieri (50)	28
132	f						Caulolatilus cyanops (10)	
133		m		f,j			Rachycentron canadum (10)	
134				j			Echeneis naucrates (20)	
135		j				j	Remora remora (2)	

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references	
136			F		j		R. osteochir (11)	
137	f j	F F	j			F	Oligoplites saurus (100)	
138		M R				F	Seriola rivoliana (20)	35
139	f	R		R		R	S. dumerili (20)	35
140		f					Decapterus punctatus(50)	
141				f			D. macarellus (50)	
142		f	f	j	f,j		Selar crumenophthalmus (50)	
143		M,f r	r	M f			Caranx ruber (100)	
144		f	F		M		C. bartholomaei (20)	35
145	po	M po	r		j	M	C. crysos (300)	
146		f f	M	R f,j			C. hippos (10)	5, 35
147	R	M,f r	M,f R	f R			C. latus (300)	35
148		r M,f			M,f		C. lugubris (50)	
149	f	M					Vomer setapinnis (50)	
150		M			j		Selene vomer	35
151		m					Hemicaranx amblyrhynchus (1)	
152			j	f	po		Alectis crinitus (10).	
153	f	j		M,f			Chloroscombrus chrysurus (100)	
154	j		j	j		j	Trachinotus falcatus (30)	
155			m		f		T. goodei (30)	
156				j		j	Elagatis bipinnulatus (10)	
157	R R	R j	f f	f	f f	F f	Coryphaena hippurus (600)	60
158		f	f		f		C. equiselis (20)	
159		j	f	f			Lutjanus cyanopterus (10)	
160		m	M	F	M		L. griseus (50)	61
161	f	r,F f	f				L. jocu (30)	35
162		f,m f			R		L. apodus (20)	5

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references
163	M	M R	R R		R		Ocyurus chrysurus (300) 54
164	f r	F F	R f	R f	f j		Lutjanus synagris (250) 62
165				F			L. mahogoni (10) 6
166	m	M,f m	r f	m			L. analis (50)
167	f,M	R			R		L. buccanella (1173) 35
168	f,M	M,f R	f	f	R	R	L. vivanus (1369) 35
169	r f,M	R R	R f				Rhomboplites aurorubens(400) 23, 35
170	f,M	R R			M		Apsilus dentatus (611) 35
171				f		f	Pristipomoides macrophthalmus(20)27
172		f j					Etelis oculatus (10) 31
173	j				M		Lobotes surinamensis (10) 48
174	F	M,f f	m R	F	F R	f	Gerres cinereus (100) 35
175				M			Eucinostomus gula (1)
176				f			E. argenteus (1)
177		M,f	f		M,f		Diapterus rhombeus (50)
178		f			f		D. plumieri (20)
179						f	D. olisthostomus (1)
180	R	R					Haemulon bonariense 35
181	f	R M,f			M,f		H. album (20) 35,54
182	F R	R M	F	R F			H. aurolineatum (300) 6,35
183	m	F					H. striatum (20) 35
184	M	R	R				H. chrysargyreum (10) 23,35
185	F	f f					H. carbonarium (10) 23,35
186		M,f f			R		H. flavolineatum (100)
187			R F	F			H. macrostomum (10) 35
188	R	f R			R		H. melanurum (10) 35
189	f		f		M		H. parrai (30)

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F		M - A		M - J		J - A		S - O		N - D		Fish species and references	
190		R	F	R					R		R		H. plumieri (100)	35
191	R	f	F									f	H. sciurus (30)	35
192	f			f	f			F			F	R	Anisotremus surinamensis (20)	6
193				R			R			R		R	A. virginicus (10)	35
194		f		f		f			f				Brachydeuterus corvinaeformis (20)	
195		f	f					j					Pomadasys crocro (50)	
196	f	f			f				M	f	M	M	Conodon nobilis (50)	
197		f	m,f										Calamus penna (20)	
198		f	f										C. pennatula (50)	
199		R	M,f		F						M	M,f	Archosargus rhomboidalis (500)	35
200	yr		yr		yr		yr		yr		yr		Cynoscion jamaicensis (20)	63
201			f			r			f				Larimus breviceps (30)	
202							f						Odontoscion dentex (100)	
203							M						Bairdiella sanctaeluciae (1)	
204	F	f	F		F		F			F	f	F	B. batabana (50)	35
205									f			f	Ophioscion adustus (10)	
206						f		M					Micropogon furnieri (20)	
207				F			F	f	F				Equetus punctatus (20)	35
208					f				M				Stellifer stellifer (100)	
209	M	M,f	R	po					j	M			Pseudupeneus maculatus (200)	35
210								R					Upeneus parvus (5)	64
211		M	F	f	F		j						Mulloidichthys martinicus (50)	35
212					R		j	j	M,R		j		Chaetodipterus faber (30)	35
213			j	f	j				po	po		j	Chaetodon capistratus (100)	
214				f									C. striatus (50)	
215				f									C. sedentarius (20)	
216					F								C. ocellatus (10)	35

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references	
217		po j					Prognathodes aculeatus (5)	
218	R	M	F R				Pomacanthus arcuatus (10)	28, 35
219		m j	F j				P. paru (10)	28, 35
220	F	f	F		j		Holacanthus tricolor (10)	35
221	R	f R		R		j	H. ciliaris (10)	35
222		j					Kyphosus sectatrix (1)	
223	j	j					K. incisor (10)	
224			R	R			Eupomacentrus adustus (10)	27
225	R	em	em R		R		E. fuscus (20)	35
226					f		E. leucostictus (20)	
227	yr	yr	yr	yr	yr	yr	E. partitus	65
228	r,j	R				R j	Abudefduf saxatilis (30)	6, 35
229			j		em		A. taurus (20)	28
230			M,f				Chromis multilineata (50)	
231		M					C. cyanea (1)	
232		f					Microspathodon chrysurus	5
233	po j	j	j	m	R f	f M,f	Mugil curema (300)	
234	f						M. liza (1)	
235					R	j	Joturus pichardi (1)	66, 80
236			M,f	f	po	j	Agonostomus monticola (100)	
237	j f	M,f M	f	F	M,f j	j	Sphyraena barracuda (300)	
238		f	f				S. guaguancho (10)	
239		f					S. picudilla (10)	
240		j j	F		f j		Polydactylus virginicus (100)	35
241			F				P. oligodon	67
242	f M,f	F				f	Lachnolaimus maximus (10)	35
243	F						Bodianus rufus (10)	

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references
244	yr	yr	yr	yr	yr	yr	Thalassoma bifasciatum (50) 68
245				R			Halichoeres buvittatus (50) 27
246		F R				F	H. radiatus (10) 28,35,69
247			R	R			Doratonotus megalepis 27
248		F				F	Hemitripterus martinicensis 70
249						F	H. splendens 70
250	R	R	R			R	Sparisoma viride (20) 35
251	R		R			F	S. aurofrenatum (4) 35
252						F	S. radians (1)
253	F m,F		M	f		f	S. rubripinne (16) 35,69
254			R	R			Cryptotomus roseus 27
255	R		f M		F	m	Sparisoma chrysopterum(100) 35,69
256		j					Scarus coelestinus (10)
257	R	R	R	R	R		S. croicensis 35,69
258	F						S. taeniopterus 35
259			R	R			S. guacamaia (30) 71
260	F f		F f	F			S. vetula (10) 35,69
261			em				Opistognathus whitehursti 1
262		em					O. maxillosus 1
263		EM					Dactyloscopus tridigitatus 1
264			R	R	po		Ophioblennius atlanticus (1) 27
265		em				EM	Hypleurochilus aequipinnis (15)
266			F	F			Emblemaria pandionis 27
267			F	em			Acanthoemblemaria aspera 27
268			em				Hemiemblemaria simulus 27
269					f		Labrisomus nuchipinnis (1)
270			M				L. bucciferus (1) 1

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references
271			F				Malacoctenus macropus 27
272					F		M. aurolineatus 72
273						F	M. erdmani 72
274		F					M. delalandi 23
275		nu		nu			Evorthodus lyricus (2)
276						nu	Gobionellus boleosoma (6)
277		M	f	M,f	po	f	Awaous taiasica (100)
278		f		f			Ginsburgellus novemlineatus (20) 38,73
279		nu		po	PO nu	po	Sicydium plumieri (1000) 74
280			f f				Gobiosoma evelynae (10) 73
281					f		Varicus bucca 75
282	em						Coryphopterus glaucofraenum (20)
283	f		f				Barbulifer ceuthoecus 73
284		f					Nes longus 73
285						j	Erotelis smaragdus (1)
286				r j	j	j	Eleotris pisonis (50)
287	j	j	m	F		m f	Dormitator maculatus (100)
288			f	f nu		j	Gobiomorus dormitor (200)
289	po R	j m				M	Acanthurus bahianus (300) 35
290	R	f,m f		R			A. caeruleus (100) 35
291	R		R				A. chirurgus (50) 35
292						f	Gempylus serpens (1)
293	f						Promethichthys prometheus (1)
294		F				m	Ruvettus pretiosus (2)
295	M,f	f					Trichiurus lepturus (50)
296			M	j	M		Thunnus albacares (3)
297			M				T. alalunga (10)

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F		M - A		M - J		J - A		S - O		N - D		Fish species and references	
298			m	m,f	f	f	m,f		R	m,f	M		T. atlanticus (200)	
299	*												T. thynnus (2)	
300	M					m							Auxis thazard (2)	
301	r	r	M,f	r	M,f	f	f	f	M	R		r	Euthynnus pelamis (50)	
302					R	M,f	f	f	f	r			E. alletteratus (50)	
303						m,f	M	f	M	f			Acanthocybium solanderi (30)	
304				f	M,f	R	R	R	f		m		Scomberomorus cavalla (100)	
305	M			M	R		f	j	F	M	M,f	M	S. regalis (100)	
306	j		j		j	j							Xiphius gladius (4)	
307					po								Istiophorus platypterus (1)	
308			m	m	f	M		M	R	M	po		Makaira nigricans (600)	
309			f	f	f								Tetrapterus albidus (50)	
310												f	T. pfluegeri (1)	
311		j		po									Psenes cyanophrys (20)	
312			j			j							Nomeus gronovii(16)	
313			M										Peprilus alepidotus	5
314						po							Bothus ocellatus (6)	
315				R									B. lunatus	77
316							R						Achirus lineatus	78
317		F,j	f	M	F		F						Balistes vetula (100)	28,35
318		j	j	j	j	j				j		j	B. capriscus (50)	
319										J	J	j	Xanthichthys ringens (200)	79
320		po		M,f									Melichthys niger (15)	
321				M,f									Canthidermis sufflamen (2)	
322				F			F	j			F		Alutera schoepfi (5)	35
323					F							F	A. scripta	35
324		j	j	R	R	j	j		j		j		Cantherines pullus (500)	35

SEASONAL SPAWNING INDICATIONS FOR FISHES FROM THE N. E. CARIBBEAN

No.	J - F	M - A	M - J	J - A	S - O	N - D	Fish species and references	
325		F					C. macroceros	
326		f					Acanthostracion quadricornis	1
327				F			A. polygonius	35
328		f			f		Lactophrys trigonus (18)	
329	f	f po		po	po	po	L. triqueter (20)	
330			F				L. bicaudalis	35
331	j			j		j	Sphaeroides spengleri (100)	
332	r			f		j	S. testudineus (50)	
333		m	j		j		Lagocephalus laevigatus (30)	
334	F	F	j	j		j	Diodon hystrix (50)	35
335	po						Mola mola (1)	
336		po					Masturus lanceolatus (1)	
	FRESHWATER FISHES							
1			R po				Dorosoma petenense	
2			f				Ictalurus punctatus	
3	f	f					I. marmoratus	
4	f						I. catus	
5	f						I. nebulosus	
6					f		Carassius auratus	
7		nu	po				Barbus conchonius	
8	j						Pimephales promelas	
9	R R	R R		R		R	Micropterus salmoides	
10		R R					M. coosae	
11	R	R	R	R	F M	f,m	Lepomis macrochirus	
12	nu,R	R	M				L. microlophus	
13		M	M				L. auritus	
14	j	r	R,po	R	R M		Cichla ocellaris	

LARVAL ENGYOPHRYS SENTUS GINSBURG, 1933 (PISCES, BOTHIDAE) FROM THE AMERICAN MEDITERRANEAN SEA

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CONTENTS

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2. MATERIALS AND METHODS
3. DESCRIPTION OF LARVAL STAGE
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5. IDENTIFICATION
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Abstract

The structure of 15 larval Engyophrys sentus, 2.4 to 11.2 mm standard length, caught in the Gulf of Mexico and in the Caribbean Sea in August 1969 and February-March 1971 and 1973, was studied. The larvae of this species are described for the first time; they have the following characteristic features: spines on the urohyal, posterior process of the pelvic, the cleithrum and the otic bones; the base of the left ventral fin is somewhat wider than that of the right. The first ray of the latter is at the level of the space between the first and the second rays of the left ventral fin. Small larvae of this species have a markedly elongated ray of the dorsal fin and are weakly pigmented: they have spot-like melanophores in the lower part of head and trunk. As the larvae grow they lose their black pigment. During development the changes in body proportions are almost similar to the larvae of Bothus.

The data on larvae of sinistral flounders, which have the same serration as larval Engyophrys, are analysed and it is supposed that the genus Engyophrys as well as the genus Taeniopsetta (Amaoka, 1969) is much closer to the subfamily Bothinae than to the subfamily Paralichthinae, to which these genera were attributed earlier (Norman, 1934).

Resumen

Se ha estudiado la morfología de 15 larvas de Engyophrys sentus de 2,4 a 11,2 mm de longitud (estandard) capturadas en el Golfo de México y en el Mar Caribe en agosto de 1969 y febrero-marzo de 1971 y 1973. Es la primera vez que se procede a una descripción de larvas de esta especie. Sus características son las siguientes: espinas en el urohyal, en la apófisis posterior del pélvico, en cleithrum y en los huesos óticos; base de la aleta ventral izquierda más ancha que la de la derecha. El primer radio de esta última se encuentra a la altura del intervalo entre el primero y el segundo radios de la aleta ventral izquierda. Las larvas pequeñas de esta especie tienen un radio muy alargado en la aleta dorsal y su pigmentación es débil: tienen melanoforas punteadas en la parte inferior de la cabeza y el tronco. A medida que las larvas crecen, pierden la pigmentación oscura. Durante el desarrollo, los cambios en las proporciones del cuerpo son casi análogos a los de las larvas de Bothus.

Se analizan los datos relativos a platijas sinistrorsas, que tienen el mismo armamento espinoso que las larvas de Engyophrys, y se hace la hipótesis de que el género Engyophrys y el género Taeniopsetta (Amaoka, 1969) estén mucho más próximos a la subfamilia Bothinae que a la subfamilia Paralichthinae, a la que se atribuían anteriormente estos géneros (Norman, 1934).

1. INTRODUCTION

The genus *Engyophrys*, which is endemic to the seaboard of the American continent, includes two species - *E. sancti-laurentii* Jordan and Bollman and *E. sentus* Ginsburg (Ginsburg, 1933; Norman, 1934). The former was found along the Pacific coast of Central and South America; the distribution of the latter is along the shelf of the Atlantic coast of America, from Florida to Brazil (Norman, 1934; Gutherz, 1967). One more species of this genus from the central Atlantic, *E. ciliaris* (Roux, 1968), has recently been described; however, Staiger (1973) considers this species to be synonymous with *E. sentus*.

In the region investigated, *E. sentus* was found in the Florida Keys, the Gulf of Mexico along the coast of Louisiana and Texas, on the shelf of the eastern coast of Mexico to the Yucatan Peninsula, in the Caribbean Sea along the shores of Central and South America and, in addition, in the region of the Bahamas and Bermuda (Topp and Hoff, 1972).

I found that only the paper of Ahlstrom (1971) gave information on larval *Engyophrys* with brief descriptions of characteristic features for larval *E. sancti-laurentii*. The larvae of the Atlantic species of this genus which we studied have not yet been described.

2. MATERIALS AND METHODS

One thousand three hundred and sixtynine samples, collected by ichthyo- and zooplankton nets in Gulf of Mexico and Caribbean Sea (in 1962, 1964-65, 1969-71, 1973 and 1975 were at our disposal. Larval *E. sentus* were obtained only in 10 samples taken in August 1969 and February-March 1971 and 1973 (Fig. 1). A total of 15 larvae of this species was taken, varying between 2.4 and 11.2 mm standard length. Larvae were preserved in 2-5% formalin. The projecting microscope "Promar" was used to make original drawings. Before drawing, the larvae were placed in glycerol to clear the tissues. Counts and measurements of larvae were made with a binocular dissecting microscope and ocular micrometer. All measurements were made on the left side of the fish, as follows:

Standard length (SL):	tip of snout to end of notochord, or tip of hypural elements.
Pre-anal length (PAL):	tip of snout to a perpendicular through anus.
Head length (HL):	tip of snout to posterior opercular margin.
Body depth (BD):	depth measured vertically from anus to dorsal fin base.
Eye diameter (ED):	horizontal measurement of left eye.
Snout length (r):	anteriormost part of premaxillary to anterior edge of left eye.

For descriptions of larvae the following were recorded:

l - length of elongated ray of dorsal fin; D, A and C - number of rays in dorsal, anal and caudal fins.

3. DESCRIPTION OF LARVAL *ENGYOPHRYS SENTUS* GINSBURG, 1933

The larva of 2.4 mm SL (Fig. 2) is not very deep (BD 19.2% SL), is markedly laterally compressed and is surrounded by a finfold. The number of myomeres is 10 + 28. The upper profile of the head is concave. The mouth is small, oblique and its angle is located in front of an eye. The tip of the lower jaw reaches a little in front of the tip of the upper. The length of the head is less than its depth. Eyes are very large (ED 45.3% HL). A strong pterygiophore supports an elongated ray, the length of which is a little more than half that of body (51.1% SL) and is located above the front part of midbrain. On the lower edge of the urohyal are the rudiments of two spines; on the cleithrum, in its lower part,

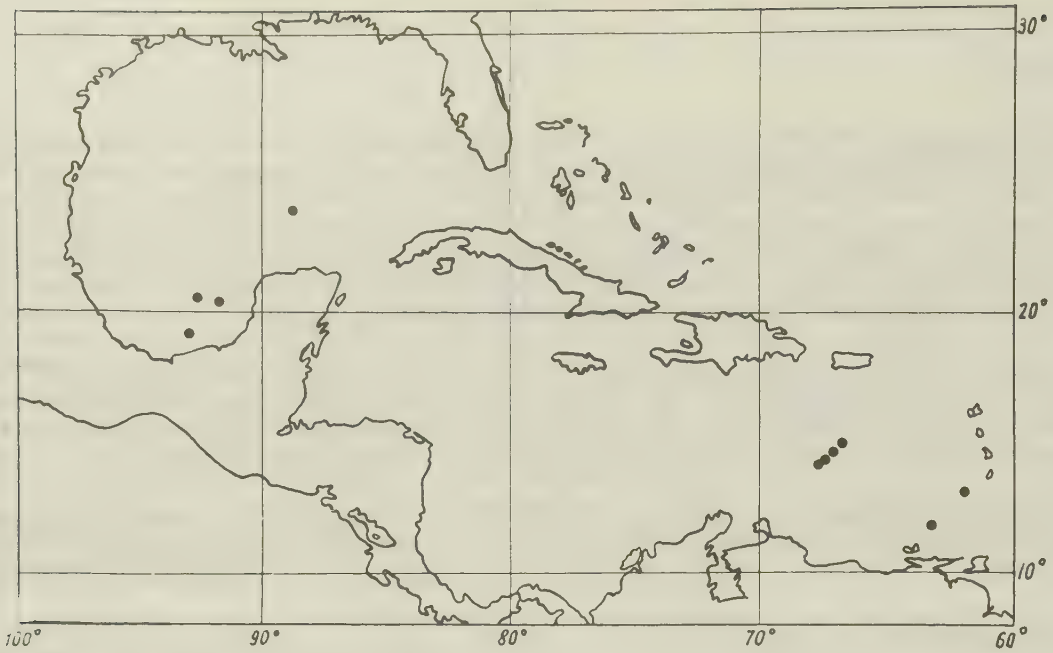

30°
20°
10°
100°
90°
80°
70°
60°

Fig. 1 Collection sites of Engyophrys sentus larvae

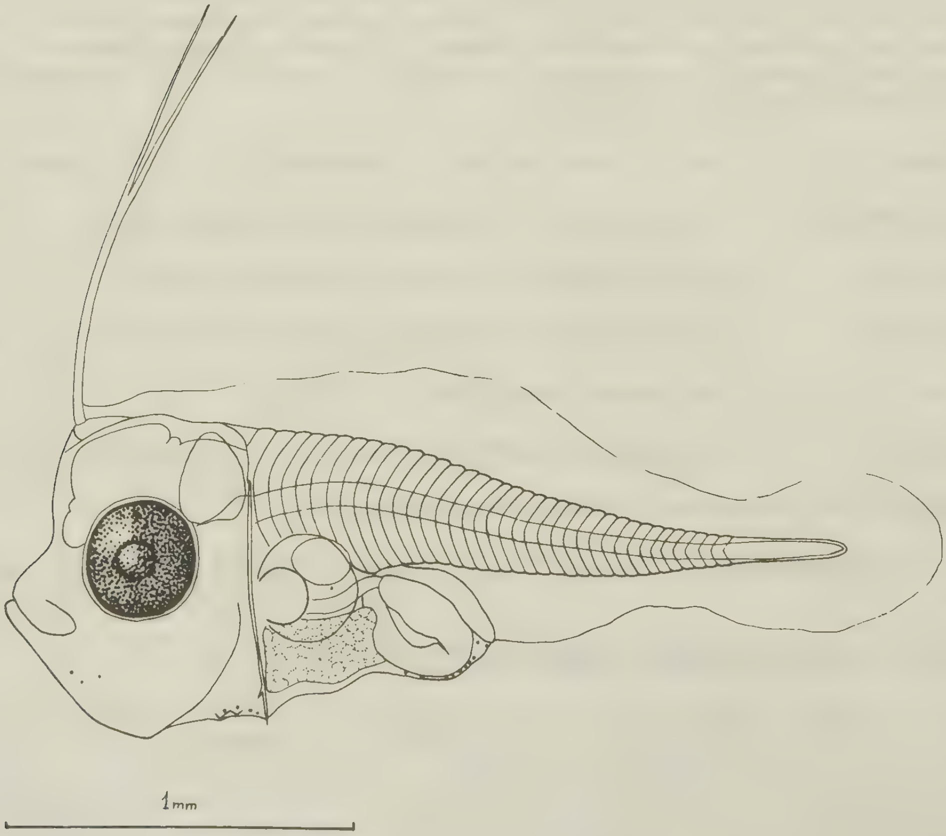


Fig. 2 E. sentus larva, 2.4 mm SL

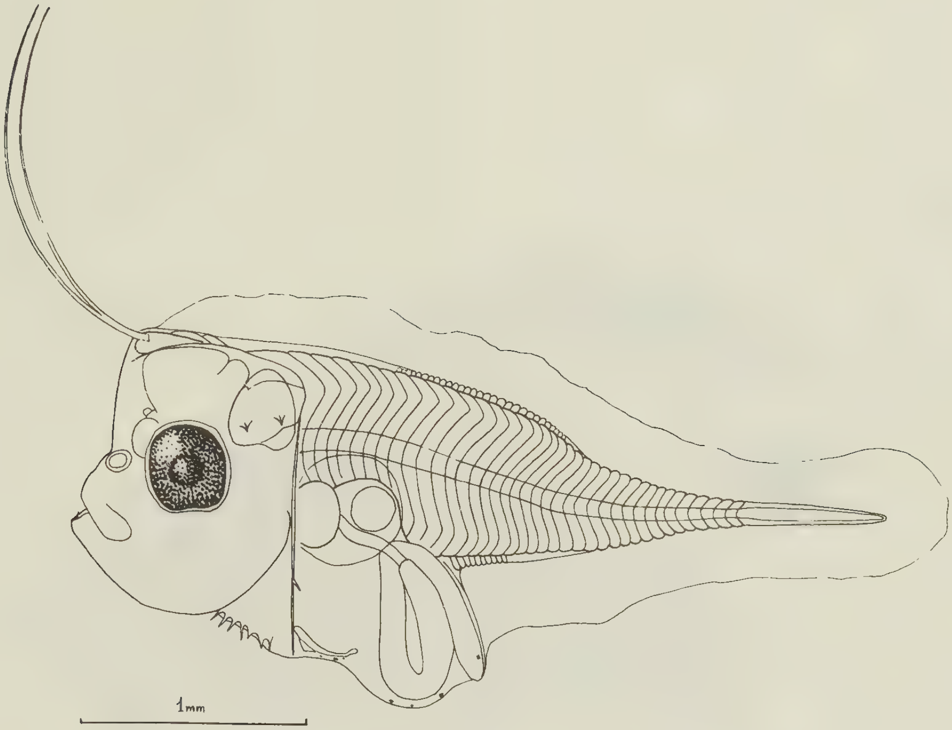


Fig. 3 *E. sentus* larva, 3.7 mm SL

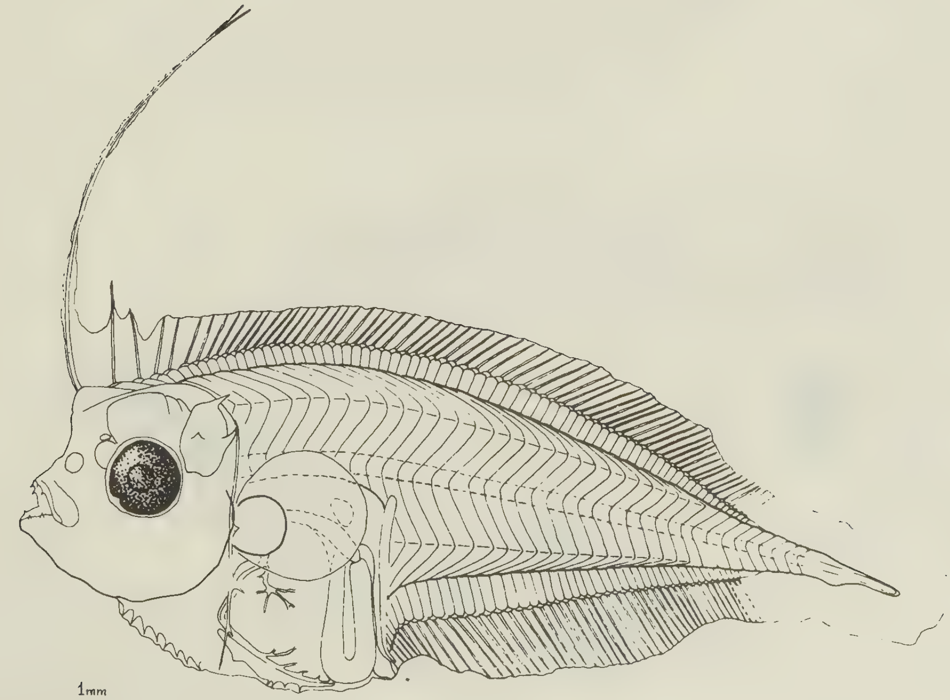


Fig. 4 *E. sentus* larva, 5.4 mm SL

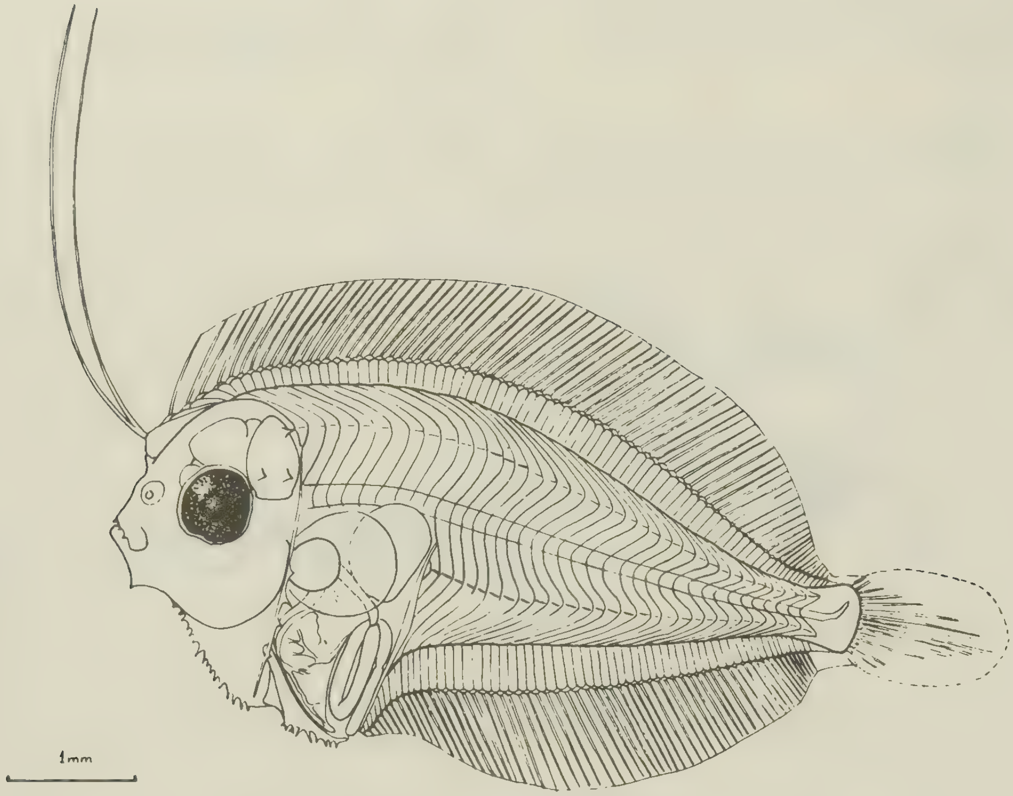


Fig. 5 E. sentus larva, 6.2 mm SL

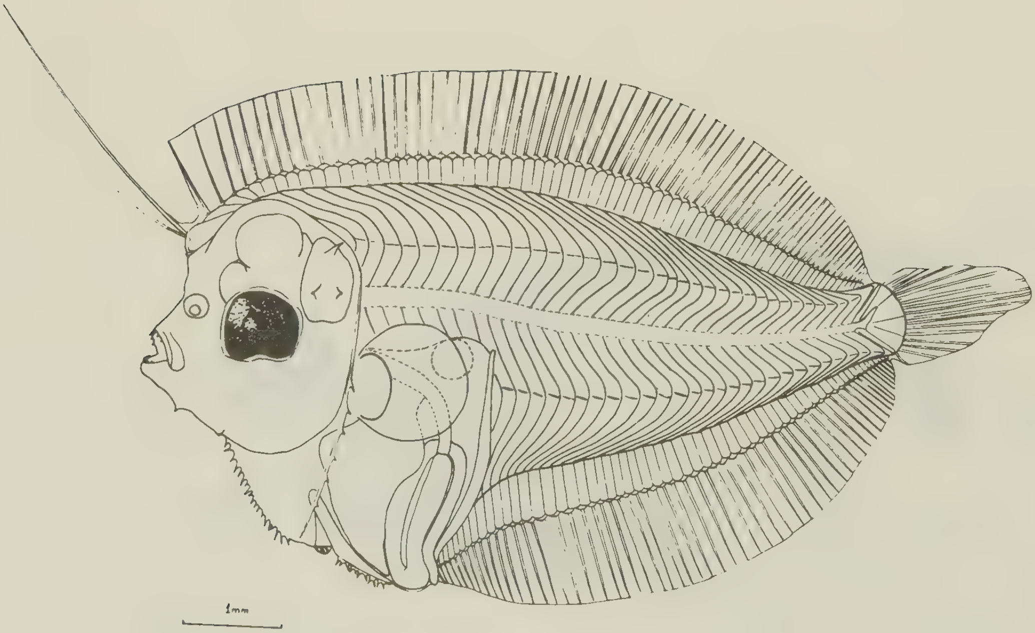


Fig. 6 E. sentus larva, 7.65 mm SL

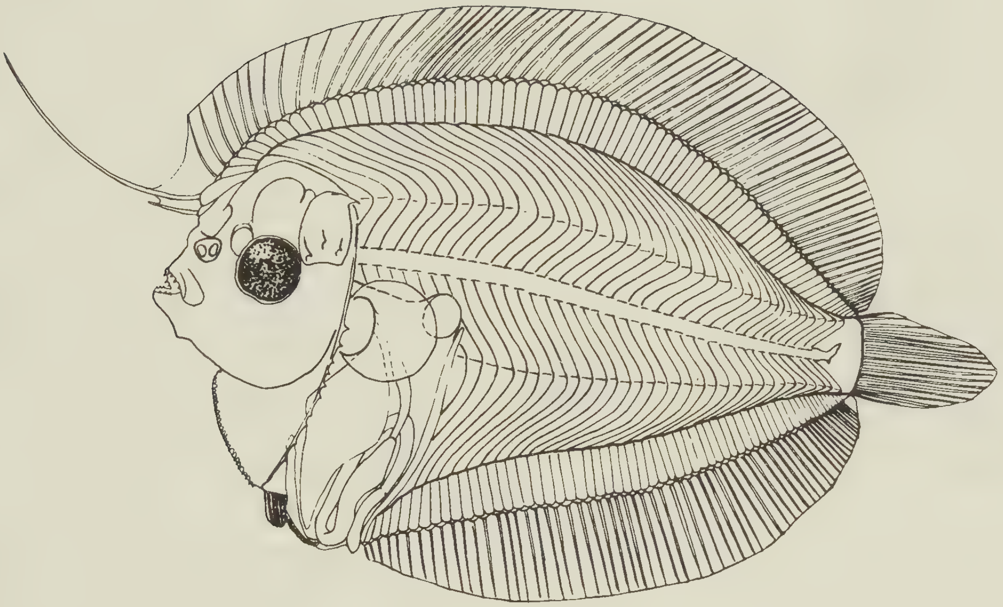
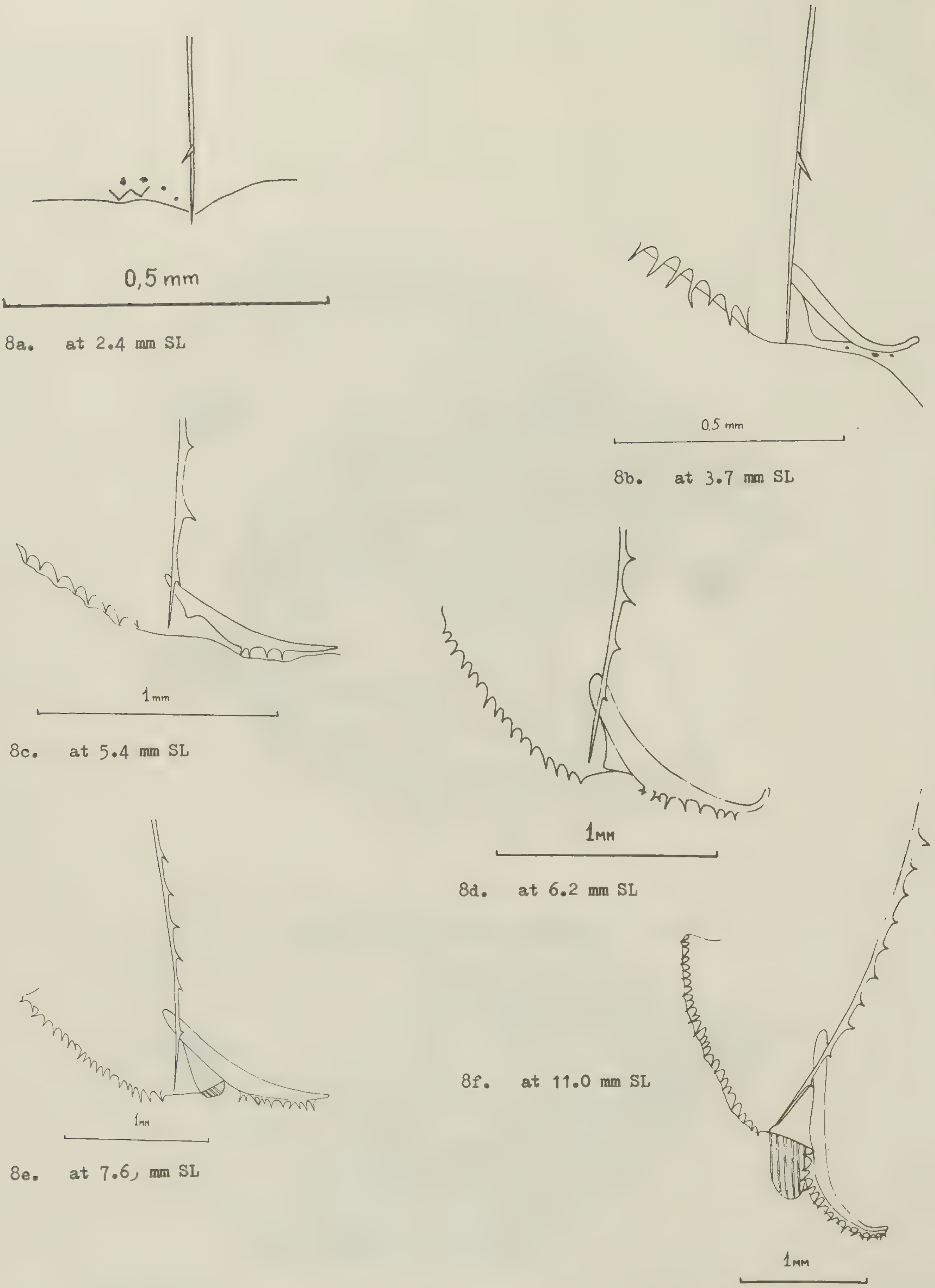


Fig. 7 E. sentus larva, 11.0 mm SL


0,5 mm
0,5 mm
1mm
1MM
1MM
1MM

8a. at 2.4 mm SL

8b. at 3.7 mm SL

8c. at 5.4 mm SL

8d. at 6.2 mm SL

8e. at 7.6, mm SL

8f. at 11.0 mm SL

Fig. 8 Developmental stages of the urohyal, Pelvic and cleithrum of **larval** ***E. sentus***

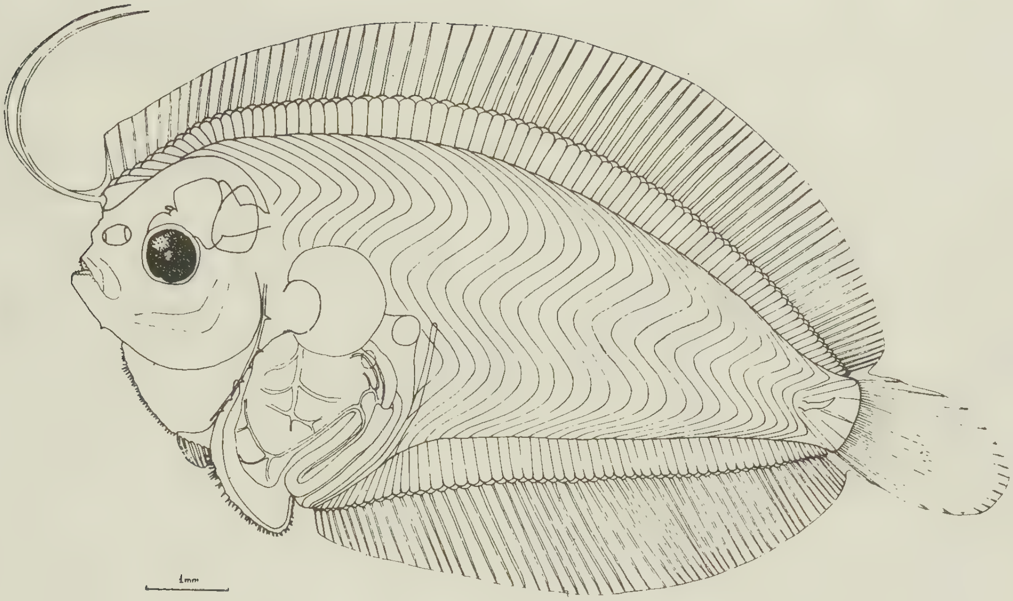


Fig. 9   Larva of **Crossorhumbus** sp. at 9.2 mm SL

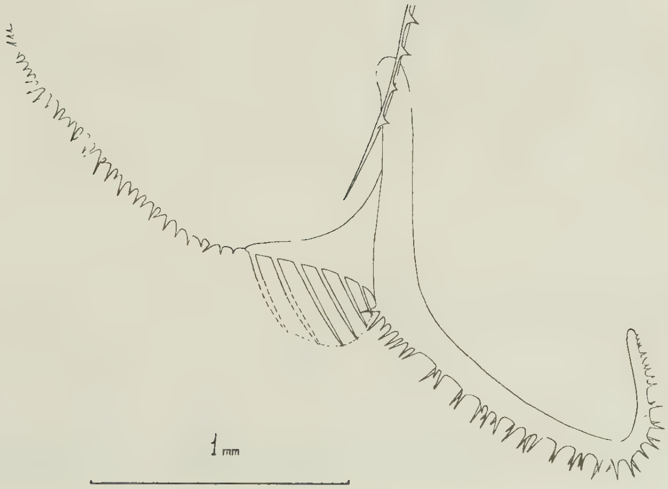


Fig. 10   Enlargement of ventral part of Fig. 9

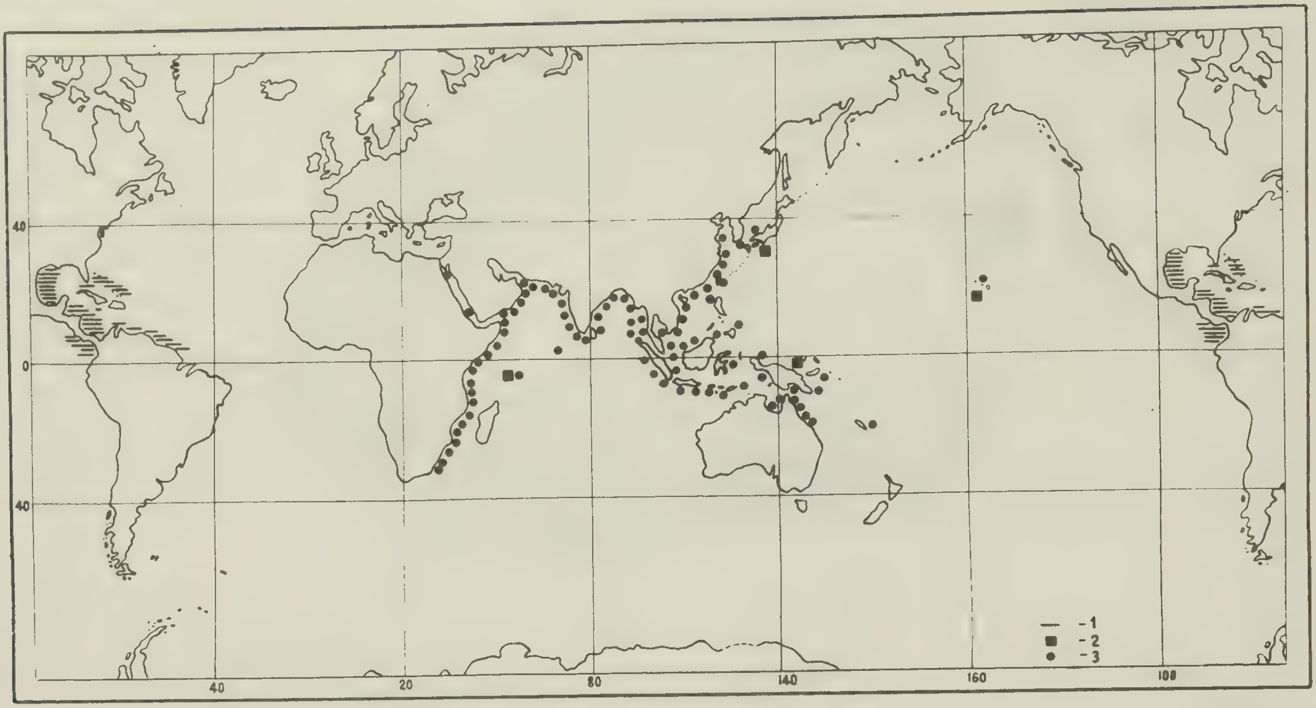

40
0
40
40
20
80
140
160
108
— -1
■ -2
● -3

Fig. 11 Distribution chart of the genera Engyophrys, Taeniopsetta, Crossorhombus, Psettina and Engyprosopon (from Norman, 1934; Botros, 1971; Topp and Hoff, 1972)

1 = Engyophrys

2 = Taeniopsetta

3 = Crossorhombus, Psettina and Engyprosopon

one spine is seen (Fig. 8a). Between the cleithrum and the intestinal loop a large, almost quadrangular, liver is located. The anus opens in the middle of the body. A rather large air-bladder is seen in the upper part of peritoneum. The larva is slightly pigmented. In the lower part of the head are spot-like melanophores; four similar pigmented cells are located on the urohyal and there is a row of eight cells under the intestine.

The body depth of the 3.7 mm SL (Fig. 3) larva, as compared with the previous one, has increased markedly (BD 35.1% SL), and the diameter of the eye decreased (ED 36.4% SL). The number of myomeres is 10 + 27 - 28. On each side of the dentary one small tooth is seen. On the dorsal edge of the body rudiments of 32 pterygiophores of the dorsal fin have appeared. Two are seen behind the pterygiophore of the first ray, others in the middle part of the upper edge of the body. On the ventral edge of the caudal part of the body 10-11 pterygiophores of the anal fin have appeared. The olfactory capsule is plainly visible. On the otic capsule are two spines sticking out perpendicular to the plane of the body. On the urohyal it is possible to count 7 spines; on the cleithrum only one as before (Fig. 8b). The rudiment of the pelvic girdle, in the shape of a curved cartilage in the upper part of which there is growth of a triangular form, is located on the lower part of the cleithrum. Three spot-like melanophores are located under this pelvic area, three others are under the intestinal loop and one melanophore is seen on the right side of the body in the lower part of the rectum.

The body of the 5.4 mm SL larva (Fig. 4) is not pigmented at all. The number of myomeres (10 + 28) is equal to the number of vertebrae. The upper profile of the head is concave and has a small projection in the region of the olfactory capsule. On the upper and lower jaws, on each side, are two small teeth. Dorsal and anal fins are not completely formed (D 65-66, A 48-49). Length of the first ray of the dorsal fin is a little larger than half body length; the remains of the finfold can be seen on it. The ventral cavity is limited behind by a massive interhaemal spine. The liver, permeated by blood vessels, occupies the space, limited below by the pelfic, above and behind by branches of the intestine. On the otic capsule three large spines stick out perpendicular to the plane of the body and three spines on the cleithrum have the same direction. On the urohyal the number of spines has increased to eight; on the lower edge of the posterior process of the pelvic are three spines, the two first being doubled (Fig. 8c).

The body depth of a larva of 6.2 mm SL (Fig. 5) has increased (BD 54.0% SL). Length of the first ray of the dorsal fin is equal to 52.5% of SL. Dorsal, anal and caudal fins are not yet completely formed (D 79, A 61-62, C 16). There are 10 + 28 vertebrae. There is a swollen air-bladder occupying not less than a quarter of the ventral cavity; stretching in a dorsal-ventral direction is pronounced. The rectum is long; its end is located lower than the base of the intestinal loop. Growth on the pelvic girdle, to which the rays of the ventral fin will be connected, has reached the lower edge of the body. On the urohyal the number of spines is now 16, the majority not on the plane of body but at different angles to it. On the cleithrum the number of spines increased up to four, on the posterior process of pelvic its number reached ten (Fig. 8d), on the otic capsule there are three spines as before.

The depth of body of a larva of 7.65 mm SL (Fig. 6) is about 54.8% SL. The relative length of the first ray of dorsal fin (40.0%) is less than in the larva mentioned above. There are 10 + 27 vertebrae. Dorsal and anal fins are completely formed (D 74, A 63). The caudal fin has 17 rays, which are connected to supporting elements in the following succession: 1-3-5-4-3-1. The rudiment of the left ventral fin, with four rays, has appeared. On the otic capsule there are 3 spines as before. On the urohyal the number of spines has increased to 20, on the cleithrum, up to 6 and on the posterior process of pelvic, up to 11. It can be seen that the spines on the posterior process of the pelvic originate from a transparent plate, knitted with the lower edge of this process (Fig. 8e).

As before, the larva of 11.0 mm SL (Fig. 7) is symmetrical and its body depth is greater than that of the previous larva (BD 63.8% SL). The upper profile of the head is almost straight, with a small projection in front of the olfactory capsule. On the upper jaw are four small teeth and, on the lower, there are three teeth on each side. There are 10 + 28 vertebrae. An additional ray has appeared in front of the elongated ray of the dorsal fin (D 80, A 63). In the pectoral, no fin rays are seen. The left ventral fin, consisting of 6 rays, is located on the edge of the body, the origin of its base being slightly in front of the cleithral tip; the right ventral fin, with six rays, is located above the edge of the body, its base starting behind the cleithrum. The first ray of the right ventral fin is level with the space between the first and second rays of the left ventral fin. The ventral cavity has increased dorsal-ventrally, the liver is now rhomboid and the translucent air-bladder is located in the right upper angle of the peritoneum. The spines on the urohyal are 27 in number, on the posterior process of the pelvic 13 and on the cleithrum 10; these latter have decreased in size and are almost buried under the skin (Fig. 8f). A fourth spine has appeared on the otic capsule.

4. DISCUSSION

Judging from our material the post-embryonic development of E. sentus has the following features: small larvae of this species do not have a deep body, are laterally compressed, have very large eyes and an elongated first ray of the dorsal fin. As the larvae grow, the depth of the body increases and, when they reach 11.2 mm SL, the depth is 68.0% SL; the elongated ray of the dorsal fin has diminished. It can be emphasized here that, in the development of larval E. sentus, the changes in body proportions noted closely resemble those observed in the development of Bothus larvae (Kyle, 1913; Evseenko, 1976). Even the smallest larva studied has spines on the rudiments of the urohyal and cleithrum and, with the appearance of supporting elements of the ventral fin, spines also appear on the lower edge of the posterior process of the pelvic. As the larvae grow, the number of spines increases although their relative size decreases; large larvae have only small spines, particularly on the urohyal and the posterior process of the pelvic, where they are buried under the skin. In addition, larvae of 3.7 mm SL and above have spines on the otic capsule. The dorsal, anal and caudal fins of larvae 7.65 mm SL and over are completely formed. At this stage the dorsal, anal and caudal fins have 74-80, 63-64 and 17 rays respectively. The 3.7 mm SL larva already has developed a pelvic in the shape of a curved cartilage; during development its front end curved upward increasingly and on the lower edge there appears a projection of triangular form, the rudiment of plate, to which the ventral fin rays will be connected. The posterior process of the pelvic elongates and is located under the massive liver, thus supporting it. The pelvic thus becomes fork-like in shape. The largest larva studied has fully formed ventral fins. The left is located on the edge of the body, its base slightly in front of the cleithrum while the right ventral fin is above the edge of the body, its first ray level with the space between the first and second rays of the left ventral fin.

Small larvae of 2.4 to 3.7 mm SL have melanophores in the lower part of the head and trunk but larger larvae are free of pigment.

There are no data on the length at which E. sentus larvae settle on the bottom; our material did not contain larvae at this stage of metamorphosis.

5. IDENTIFICATION

The larvae of at least five flatfish genera have a presence and arrangement of spines similar to the larvae studied. These genera are Crossorhombus, Engyprosopon, Psettina, Taeniopsetta and Engyophrys (Ochiai and Amaoka, 1963; Pertseva-Ostroumova, 1965; Amaoka, 1970; Ahlstrom, 1971). Of all these genera Engyophrys is the only one distributed along both sides of America. As a matter of fact the larvae of the genus Engyophrys are markedly serrated on the ventral body margin and on the otic capsule (Ahlstrom, 1971). The same arrangement of spines is also specific for larvae in our samples. Therefore they must be identified as Engyophrys species. However, the only species of Engyophrys distributed in the American Mediterranean is *E. sentus*, so the larvae described above can be assigned to this species. In addition, the vertebrae number (10 + 27 - 28) as well as the fin ray number of the dorsal (74-80) and anal (63-64) fins coincide exactly with these meristic features of adult *E. sentus* (D 71-85, A 59-69, vertebrae number 10 + 27 - 28) (Gutherz, 1967; Staiger, 1973).

6. AFFINITIES OF THE GENUS *ENGYOPHRYS* JORDAN AND BOLLMAN

Larval *Engyophrys* differ from other larvae of the subfamily Paralichthinae described in having a higher and more laterally compressed body and having spines on the urohyal, the posterior process of the pelvic and the cleithrum. On the other hand, all described larvae belonging to the other subfamily, Bothinae, have a strongly laterally compressed body similar to that of larval *Engyophrys*. Moreover, larvae of the genera *Engyprosopon* and *Psettina* bear spines on the urohyal and the posterior process of pelvic, while larval *Crossorhombus* bear spines on the cleithrum, as shown in Figs. 6a and 6b (Pertseva-Ostroumova, 1965; Ochiai and Amaoka, 1963).

The subfamily Paralichthinae includes the genus *Taeniopsetta* (Norman, 1934) which, in the opinion of Amaoka (1969), is much closer to the representatives of the other subfamily, the Bothinae. It is worth noting that larval *Taeniopsetta ocellata* (Günther), described by this same author (Amaoka, 1970), are very similar to the large larval *Engyophrys sentus* we studied in such features as shape of the body and the presence of spines on the urohyal, the posterior process of pelvic, the cleithrum and the otic capsule.

By examining the characteristics of adult *Engyophrys*, it can be seen that species of this genus, as well as *Taeniopsetta*, have a number of features in common with species of the genera *Crossorhombus*, *Psettina* and *Engyprosopon*, which belong to the subfamily Bothinae, and separate them from most representatives of the subfamily Paralichthinae, namely, the lateral line is observed only on the left side of the body and the rays of the pectoral and ventral fins do not branch (Ginsburg, 1933; Norman, 1934; Amaoka, 1969). In addition, according to one of the important features used when referring a genus to a subfamily, that is the location of the base of the ventral fins relative to the cleithrum, the genera *Engyophrys* and *Taeniopsetta* occupy an intermediate place between the Paralichthinae and the Bothinae since the origin of the base of the left ventral fin in the Paralichthinae is behind the cleithrum and, in the Bothinae, is well in front of the cleithrum (Norman, 1934). The origin of the base of the left ventral fin in *Engyophrys* and *Taeniopsetta* is but slightly in front of the cleithral tip (Amaoka, 1969; Gutherz, 1971; Author's data).

Therefore, we consider the great similarity between both larvae and, according to a number of important diagnostic features, adult specimens of compared genera from different subfamilies to have resulted from a common origin. This assumes that the genera *Engyophrys* and *Taeniopsetta* had a common, probably a flatfish-like ancestor from which living representatives of at least three genera *Crossorhombus*, *Psettina* and *Engyprosopon* also originated.

It is known that species of the above-mentioned genera, *Engyophrys* excepted, inhabit the Indo-Pacific (Fig. 11); it is probable, therefore, that this was the region their common immediate ancestor inhabited. If this be so, the question arises as to how the ancestral form reached the American continent to give rise to the present genus *Engyophrys*. I suggest that the appearance of the ancestral *Engyophrys* along the American coast was due to its passive migration, while still a larva, by way of the Equatorial Countercurrent from the West Pacific to Central America. In support of this suggestion it is reasonable to assume that the pelagic larval stage of *Taeniopsetta ocellata* is extraordinarily long and larvae are 60 mm SL at the stage of metamorphosis when they sink to the bottom (Amaoka, 1970). The appearance of a sinistral flounder of the genus *Engyophrys* in the American Mediterranean was, probably, the result of the exchange of faunas between the Eastern Pacific and the Caribbean Sea, between the end of the Miocene and the beginning of the Pliocene, prior to the formations of the Isthmus of Panama (Ekman, 1953; Khain, 1975; Rass, 1975).

7. CONCLUSIONS

1. Larval Engyophrys sentus are characterized by the following features: presence of spines on the lower margin of the urohyal, the posterior process of pelvic, the cleithrum and the otic capsule; the base of the left ventral fin is slightly wider than the base of the right, the first ray of which is level with the space between the first and the second rays of the left ventral fin; the eyes are large, the diameter being in the range 34.4-45.3% of head length. Small larvae of this species have a markedly elongated ray of the dorsal fin and are slightly pigmented; they carry spot-like melanophores on the lower part of the head and trunk, fading and disappearing in larger larvae. During development, larvae go through almost the same changes in body proportions as larval Bothus.

2. The representatives of the genus Engyophrys, judging by the peculiarities of the early stages of their development, are very close to the genus Taeniopsetta. Larvae of these genera differ notably from larvae of those species of flatfish which are included by Norman (1934) in the subfamily Paralichthinae. There is, however, great similarity in the character and arrangement of the spines in the larval Engyophrys and Taeniopsetta with larvae of the genera Crossorhombus, Psettina and Engyprosopon, which belong to the other subfamily, the Bothinae. The presence of these spines in the larvae of the above-mentioned genera is the feature which unites these genera, suggesting the inheritance of this feature from a common ancestor.

8. ACKNOWLEDGEMENTS

The author wishes to express his sincere gratitude to Professor T.S. Rass, Dr. N.S. Khromov and Dr. A.A. Dubovitsky, who provided ichthyoplankton samples for his investigations. The author also wishes to thank Professor T.S. Rass for helpful advice and criticism of the manuscript.

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INVESTIGACIONES SOBRE ICTIOPLANCTON EN EL AREA CICAR

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CONTENIDO

1. INTRODUCCION
2. PROGRAMAS Y SU DESARROLLO
3. TALLER DE ICTIOPLANCTON
4. FUTURO DE LAS INVESTIGACIONES SOBRE ICTIOPLANCTON
5. CONCLUSIONES
6. REFERENCIAS

Resumen

Las investigaciones que sobre ictioplancton se han venido realizando durante las CICAR, señalan el interés creciente que existe sobre este campo de trabajo y muestra también la necesidad de intensificarlo a través de una mayor comunicación entre los especialistas y más particularmente la necesidad de apoyo para investigadores en desarrollo en los países latinoamericanos del área.

En el presente trabajo se hace una síntesis de las investigaciones que sobre ictioplancton se han hecho a través de las CICAR, asi como de los programas que no correspondiendo a las investigaciones cooperativas contribuyen de una manera importante en el desarrollo de esta rama del conocimiento dentro del área.

Se consideran los logros, se analizan las posibilidades y se sugieren acciones, asi como también se analiza el papel del Centro de Preclasificación Océanica de México (CPOM) como apoyo para el desarrollo de este campo.

Abstract

Investigations made on ichthyoplankton during CICAR indicate the growing interest that exists in this field of work and also show the need to intensify this effort through better communication among specialists. Expansion of the ichthyoplankton work is particularly needed to support the growing number of new investigators in the countries of the CICAR area.

This paper is a synthesis of investigations on ichthyoplankton made during CICAR and of other programmes that, even though not related to the cooperative investigations, have contributed in an important way to the development of this branch of knowledge in the Caribbean.

Scientific advances are considered, future possibilities are analysed, and suggestions are made. Also, as support to the development of this field, the report of the Mexican Sorting Center (CPOM) is analysed.

1. INTRODUCCION

Las investigaciones que sobre ictioplancton se han venido realizando durante las CICAR, señalan el interés creciente que existe sobre este campo de trabajo y muestra también la necesidad de apoyo para los jóvenes investigadores en los países en desarrollo.

Por lo mismo el presente escrito pretende resumir los programas y logros de los mismos, mostrando en qué medida se han desarrollado y cuál ha sido su aspecto cooperativo.

Con este objeto se solicitó la cooperación de investigadores que trabajan sobre este campo en el área CICAR, principalmente a aquellos que asistieron al taller de trabajo sobre huevos y larvas de peces desarrollado en el Centro de Preclasificación Océanica de México en julio de 1974 a fin de obtener una información más directa y objetiva de los programas existentes en el Area CICAR, pues a través de los informes nacionales de los países al Grupo Internacional de Coordinación CICAR que cumplen con una función de información general, no puede obtenerse todo.

2. PROGRAMAS Y SU DESARROLLO

A través de los programas nacionales presentados a las reuniones del Grupo Internacional de Coordinación CICAR, por los coordinadores nacionales se puede apreciar que aquellos sobre ictioplancton comprenden sólo una fracción muy pequeña del total de programas sobre física, química y biología.

De todos los países miembros de las CICAR sólo tres han venido desarrollando programas ictioplanctónicos de una manera sistemática, incluso antes de iniciadas las actividades CICAR, y son Cuba, U.R.S.S. y EE.UU.

En Cuba particularmente y en virtud de los programas cooperativos con la U.R.S.S., se iniciaron investigaciones sobre ictioplancton desde 1964, a fin de hacer un levantamiento ictioplanctonológico de las aguas, adyacentes a la isla, de manera que en 1970, cuando se integran estos programas a las investigaciones CICAR, tienen mucho hecho sobre este campo y lo más importante ya hay personal capacitado, formado a través de la colaboración cubano-soviético, aunque ya había una formación precedente desde 1954.

Las instituciones cubanas que han venido trabajando sobre ictioplancton son el Instituto de Oceanología de la Academia de Ciencias de Cuba, abarcando principalmente la plataforma cubana y el Centro de Investigaciones Pesqueras del Instituto de la Pesca, que ha venido trabajando más en aguas oceánicas del Golfo de México y Mar Caribe.

En Cuba se ha prestado gran interés a los estudios de ictioplancton como fuente importante de información básica sobre la composición ictio-faunística, obteniendo una impresión de la abundancia relativa de las especies y de las áreas de concentración para desove con especial interés sobre aquellas de importancia comercial.

El equipo que han utilizado ha variado con el tiempo e incluso durante el primer simposium CICAR se presenta el trabajo "Un nuevo sistema para armar redes de ictioplancton" (Guitar, 1969), y se sabe cuenta ahora con equipo Bongo, lo que permitirá hacia el futuro hacer los datos comparativos con otras instituciones de otros países.

Cuba cuenta actualmente con cinco profesionistas dedicados a esta disciplina, así como dos estudiantes universitarios avanzados y seis técnicos medios.

La U.R.S.S. inició sus estudios sobre ictioplancton en el Golfo de México, Caribe y Atlántico adayacentes hasta 1964 con los programas cooperativos cubano-soviéticos, contando en ocasiones con buques oceanográficos rusos como es el caso de los B/O ALEXANDER KOVALEVSKY, AKADEMIK KURCHATOV y AKADEMIK VERNADSKY.

Se puede decir que son tres instituciones esencialmente las que han intervenido en este tipo de investigación, el Instituto de Oceanología (de la Academia de Ciencias de la U.R.S.S.), Instituto de Biología de los Mares del Sur (de la Academia de Ciencias de Ukrania) y Unión de Institutos de Investigaciones de Pesquerías Marinas y Oceanografía.

Las investigaciones se han desarrollado dentro del marco de cooperación cubano-soviético, de manera que al iniciarse las CICAR, también los soviéticos incorporaron estas investigaciones al plano CICAR.

Los principales objetivos de estos estudios han sido una revisión general sobre distribución y abundancia del ictioplancton en la vertical y en la horizontal, estudios sobre el desarrollo larval de algunas especies; particular interés se puso en el análisis de épocas y zonas de desove para algunas especies de escombridos de importancia comercial.

Un breve resumen de las actividades puede ser hecho en la forma siguiente:

Colectas ictioplanctónicas del Instituto de Oceanología a través del crucero realizado por el B/O ALEXANDER KOWALEVSKY en 1965, análisis de localidades y época de desove para diez especies de escombridos a través de colectas hechas con pequeños botes cubanos sobre la plataforma insular.

Incubación experimental, fertilización de huevos tomados de peces maduros a fin de obtener su desarrollo y poder llevar a cabo una identificación correcta de los huevos pelágicos.

Colectas ictioplanctónicas a través del crucero con el B/O AKADEMIK KURCHATOV en 1973 principalmente en mar abierto.

Entre las actividades desarrolladas por el Instituto de Biología de los Mares del Sur, destacan los cruceros realizados en 1971-72, 1972-73 por el B/O AKADEMIK VERNADSKY de cuyos materiales se han desarrollado una serie de trabajos, como los de la Dra. I. Deknik.

El equipo que se ha venido empleando ha sido muy variado tal como redes para zooplancton, red cónica para ictioplancton, Isaacs Kidd, Bongo, etc.

Si bien no podemos saber cuantas personas laboran en la U.R.S.S. sobre ictioplancton, se puede estimar que por lo menos diez o doce investigadores han venido trabajando constantemente sobre el área CICAR incluso antes de iniciar estas investigaciones cooperativas del área.

El tercer país mencionado, que ha llevado a cabo investigaciones sistemáticas del ictioplancton del área CICAR, es EE.UU. que sin duda en virtud de ser un país limítrofe de esta área y con mayores recursos, ha sido quien mayores esfuerzos ha puesto en este campo.

La parte más importante de las investigaciones ictioplanctónicas, la han desarrollado a través del programa Marine Resources Monitoring, Assessment and Prediction (MARMAP) del U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, National Marine Fisheries Services. Dentro de este programa dos investigaciones ictioplanctonológicas fueron llevadas a cabo en el marco CICAR durante julio y agosto de 1972, y enero y marzo de 1973, a los que se llama "MARMAP Operational Test Phase " (OTL), cuyos objetivos fueron determinar la distribución y abundancia de huevos y larvas de peces de importancia, tanto de pesca deportiva como comercial. Dentro de estos objetivos estuvo también el conocer el efecto de las principales corrientes tales como la del Golfo, sobre la distribución de huevos y larvas y las correlaciones entre nutrientes y concentraciones de ictioplancton. Algunos trabajos han resultado ya de estas investigaciones pero mucho está apenas en proceso.

Esta labor se llevó a cabo con la participación de varios buques oceanográficos tales como ALBATROS IV, DELAWARE II, OREGON II, DOLPHIN, TRIDENT y WIECZNO, pertenecientes a diversas instituciones.

Entre otros programas importantes que han venido desarrollándose, está el de la Universidad de Miami, el cual comenzó en 1970 junto con los de MARMAP OTL habiendo cubierto actualmente 17 cruceros y 880 muestras, de este material sólo los clupeidos han sido estudiados (Houde, 1973, y otro en prensa) estando el resto en proceso.

La periodicidad mensual de los muestreos ha dado gran cantidad de información sobre la localización de existencias, área y época de desove.

Otro programa más ha sido desarrollado por Texas Coast por el Bureau of Land Management of U.S. Department of the Interior, como base de estudio de recursos marinos vivientes en áreas externas de exploración y explotación de petróleo.

El Marine Biomedical Institute de la Universidad de Texas inició en 1975 un programa de más particulares objetivos como son: distribución, abundancia y variación estacional de larvas leptocéfalas en el Golfo de México y otros aspectos de tipo fisiológico sobre las mismas.

Anterior a CICAR se pueden citar una serie de investigaciones periódicas sobre ictioplancton como la del Department of Natural Resources del Estado de Florida 1965-67 sobre la plataforma continental y otras investigaciones sobre medios estuarinos.

En el Mar Caribe, se han realizado investigaciones por el National Marine Fisheries Service, Laboratorio de Miami, desde 1963 a 1971, particularmente para el estudio de larvas de atunes, aunque ningún resultado ha sido publicado.

Por otro lado, la Universidad de Miami ha colectado plancton a través del área CICAR, durante los últimos 25 años, aunque de ninguna de estas muestras ha sido estudiado el ictioplancton en virtud del alto costo de separar los huevos y larvas de peces y de lo complejo que resulta la identificación de las especies.

El equipo empleado ha sido también variado, aunque dentro de los programas CICAR fue el único país que siempre pudo emplear la red Bongo y Neuston que se recomendó.

No es posible estimar cuantas personas trabajan sobre ictioplancton en EE.UU., pero al menos para el área CICAR, cerca de 15 investigadores han trabajado en este campo durante los últimos 15 años, además de muchos otros con carácter pasajero u ocasional.

Un país que trabaja en forma sistemática sobre ictioplancton es Brasil, particularmente el Instituto Oceanográfico de São Paulo, aunque sólo una pequeña parte de sus trabajos involucran el área CICAR. Vale la pena mencionar que en los últimos ocho años han desarrollado al menos 20 cruceros principalmente con la ayuda de los B/O PROF. W. BERNARD y EMILIA. Sus principales objetivos han sido enfocados al conocimiento de la biología y distribución de algunas especies de interés comercial, trabajando actualmente diez personas en este campo.

El resto de los países miembros del área CICAR no tienen programas ictioplanctonológicos en el área o estos son pequeños y con pocas posibilidades de un rápido desarrollo en la medida que al frente de ellos están investigadores a quienes hace falta la base o apoyo de investigadores experimentados, además de equipo y bibliografía.

En México sólo el Instituto Nacional de Pesca ha trabajado en este campo y sus principales objetivos están enfocados actualmente a especies de interés comercial en la costa Pacífica del país. No obstante y como resultado específico de los programas cooperativos CICAR, a través de los cruceros con el B/O VIRGILIO URIBE en 1971 y 1972, realizaron estudios tendientes a conocer la distribución, geografía de los estadios larvarios (y adultos) de peces pelágicos de importancia comercial, principalmente en el Golfo de México, cuyos resultados han sido ya publicados.

El equipo empleado en estos trabajos fue una red de Neuston, con marco rectangular de 2 x 1 m y 9 m de largo, como se recomendó para las CICAR. Con el objeto de calibrar las redes y estandarizar el trabajo el crucero VU/71/02 se efectuó junto con el B/O OREGON II del Bureau of Commercial Fisheries de EE.UU.

Actualmente el único programa ictioplanctónico en el área CICAR es desarrollado por el Centro de Ciencias del Mar y Limnología de la UNAM, en la Laguna de Términos (Golfo de México) iniciado recientemente.

México cuenta actualmente con diez investigadores en este campo, muchos de ellos en desarrollo, además de cinco técnicos que desempeñan una función de servicio en el Centro de Preclasificación Oceánica de México.

De los Centros de Investigación en Jamaica unicamente la Universidad de Indias Occidentales inició un programa sobre ictioplancton en 1973 cuyos objetivos fueron determinar las fuentes de reclutamiento de las existencias de los peces de los arrecifes de Jamaica y los ciclos de vida de algunas de estas especies, a través de un programa de muestreo bisemanal. No existe a la fecha nada publicado sobre estos trabajos, en virtud de factores tales como la dificultad de identificación del material y falta de personal. Jamaica cuenta actualmente con sólo dos investigadores en este campo.

Venezuela ha venido trabajando sobre ictioplancton particularmente sobre algunas especies de interés comercial, incluso con antelación a CICAR, y en sus programas presentados al GIC-CICAR en 1973 tienen programados estudios de huevos y larvas de peces dentro del proyecto pesquerías y biología de peces.

Colombia en su informe al GIC-CICAR en 1973, señala colectas sobre huevos y larvas de peces que enviaron posteriormente al Centro de Preclasificación de México (no se recibieron), pero no existe un programa definido.

Francia dentro de sus proyectos para 1974 tuvo el de crear el Centro de Investigaciones de las Antillas y en los planes de investigación aparece el estudio del ictioplancton en el talud continental de las Antillas y Guayana.

Países Bajos, dentro de un plan general de estudio de las comunidades planctónicas del área CICAR, comprenden el estudio de ictioplancton del que muestran algunos adelantos en su informe de 1971.

Desgraciadamente no se obtuvo respuesta acerca de los proyectos, personal y otro tipo de información en forma directa de Colombia, Panamá y Venezuela para poder definir mejor su estado actual y posibilidades en futuros programas. También se carece de información sobre otros países.

Ha sido señalado en el seminario sobre ictioplancton que la metodología es un aspecto fundamental, pero es claro que no todos los países tienen las posibilidades de emplear las redes Bongo que han sido recomendadas para las CICAR; el Dr. R. Marak del programa MARMAP (EE.UU.) ofreció proporcionar tal equipo a los países del área que carezcan de ella. La red Neuston sin embargo parece ha sido más ampliamente empleada.

3. TALLER DE ICTIOPLANCTON

Dentro de los aspectos cooperativos de mayor significación nacidos de las CICAR, están los seminarios que sobre distintos temas se han realizado. Sobre este tópico, se desarrolló en México del 17 al 26 de julio de 1974 un seminario sobre ictioplancton, del que se ha publicado un informe en el número 20 de los Documentos Técnicos de la Unesco sobre Ciencias del Mar (1975) donde se señalan claramente los objetivos:

"La reunión tenía por objeto examinar los adelantos recientes en los estudios de huevos, larvas y formas juveniles de peces de las aguas tropicales del Oceáno Atlántico, con especial atención a la zona de las CICAR. El seminario debería ser principalmente educativo mediante la determinación de nuestro conocimiento colectivo sobre el ictioplancton de las aguas tropicales del Atlántico y los problemas que en el se plantea. Se pidió a los oradores invitados que diesen conferencias y demostraciones sobre las diversas fases de la investigación del ictioplancton. Se hizo hincapié en el trabajo práctico de laboratorio, en examen de los problemas de identificación y la metodología del tratamiento de datos sobre ictioplancton. Se restringió la presentación de comunicaciones sobre investigación individual, dando preferencia a la libre discusión entre los participantes para definir problemas y esbozar las correspondientes soluciones."

Como se señaló, el seminario debería ser principalmente educativo ya que la experiencia de muchos de los investigadores invitados, su conocimiento de los problemas, discusión y puntos de vista, deberían redundar en un aprovechamiento inmediato para los jóvenes investigadores participantes, primordialmente en aspectos taxonómicos ya que aunque las investigaciones ictioplanctónicas comprenden también problemas de tipo fisiológico, ecológico, biológico, el más serio vacío es el reconocimiento específico de los estadios larvarios.

Dentro de las observaciones y recomendaciones del seminario, vale la pena destacar lo que el consenso de la reunión definió como los objetivos de investigación ictioplactónica en la región CICAR.

"Obtener los conocimientos básicos necesarios sobre la taxonomía, la distribución y la ecología de este importante componente de la comunidad planctónica."

"Utilizar los datos cuantitativos reunidos durante las campañas de ictioplancton para explorar nuevos recursos pesqueros y determinar la distribución y abundancia relativa de las especies de importancia económica."

"Complementar nuestros conocimientos de la dinámica de las poblaciones de peces y a ser posible, aplicar los resultados de los estudios sobre huevos y larvas de peces a la estimación de la biomasa en desove y a la predicción del reclutamiento."

Es fundamental para alcanzar tales objetivos, la correcta identificación del material ictioplanctónico.

Los resultados del taller en el plano científico, rindieron frutos inmediatos para los jóvenes participantes, aunque limitados por el propio tiempo de la reunión. No obstante, se consideró que las investigaciones futuras en este campo avanzarán más rápidamente no sólo por la información intercambiada sino también por los contactos personales establecidos por los especialistas de los diferentes países.

Así mismo para coadyuvar en este desarrollo, los investigadores acordaron que en el futuro enviarían al CPOM los ejemplares identificados de huevos y larvas de peces de su zona geográfica.

Se recomendó que las organizaciones internacionales colaborasen en la organización de un segundo seminario sobre ictioplancton en las mismas regiones geográficas, que se celebraría dentro de algunos años, a fin de evaluar los progresos realizados en este campo de la investigación.

Del resumen de los temas tratados debemos destacar algunos puntos:

"La comparabilidad de los datos cuantitativos entre diferentes regiones pesqueras es el requisito previo esencial de los programas de campañas cooperativas. Se recomendó la red Bongo de 60 cm de diámetro con malla de 0,505 mm como red normalizada para los conocimientos de ictioplancton en la región de las CICAR."

Esto resulta altamente significativo ya que como hemos podido apreciar el equipo utilizado en el área ha sido heterogéneo, lo que resta valor en el sentido comparativo.

"Se consideró que una solución neutra de formol al 4 por ciento es el fijador más adecuado para los huevos y larvas de peces de las regiones tropicales. Aspecto que resulta de suma importancia, pues la poca literatura a nivel específico para estos estadios requiere de su mejor conservación."

"En la región de las CICAR están representadas unas 180 familias de peces. Los resultados de las sesiones taxonómicas demostraron que, en la actualidad, es posible identificar las larvas de la mayor parte de esas familias, pero que se conocen los huevos sólo de muy pocas. Es sumamente incompleta la información disponible por debajo del nivel de familia."

Todo lo anterior nos lleva a una conclusión también vista en el seminario y es que los muestreos de ictioplancton, la separación y la identificación de huevos y larvas y el análisis subsiguiente de los datos debe continuarse en la región CICAR.

4. FUTURO DE LAS INVESTIGACIONES SOBRE ICTIOPLANCTON

El futuro de las investigaciones sobre ictioplancton en el área CICAR está condicionado en su crecimiento a varios factores y los principales son:

(a) embarcaciones adecuadas
(b) equipo adecuado
(c) bibliografía disponible
(d) cooperación internacional
(e) personal capacitado

Los programas que hasta ahora se han desarrollado por parte de Cuba, U.R.S.S. y EE.UU., en forma planificada en tiempo y espacio y con equipo humano y científico adecuado, seguramente continuarán, teniendo en cuenta el interés que han demostrado los mencionados países en la investigación del ictioplancton de la región; es muy posible que se amplien en razón de la aceptación de las 200 millas, en el plano internacional, como mar territorial.

Algunos países como Cuba tienen planes para extender geográficamente sus estudios a otras áreas de interés, tanto desde el punto de vista de los conocimientos básicos del ictioplancton, como de los aspectos de la potencialidad del recurso y de la evaluación de las existencias de peces, mediante el estudio de sus huevos y larvas.

La U.R.S.S., a través de la Unión de Institutos de Investigaciones de Pesquerías Marinas y Oceanografía, proyecta estudios sobre los primeros estadios de algunos Bothidae, Carangidae y otras familias presentes en el área CICAR.

Por otro lado es incierta la posibilidad de que se inicien programas que contemplen un análisis sistemático del ictioplancton en el resto de los países, pues la carencia de embarcaciones y equipo adecuado, la falta de bibliografía, particularmente a nivel de especie y la escacez de personal capacitado, es lo que más resalta.

Por lo anterior las vías que surgen más probables para el mejor desarrollo de este campo de investigación son:

(i) Formación de personal a nivel universitario en todos los países del área, a través de becas para perfeccionarse en centros calificados lo cual cubriría una deficiencia primordial y que es prerequisito para el desarrollo de los puntos siguientes,

(ii) Concentración del material bibliográfico sobre ictioplancton, al menos, en una institución de cada país y sin la cual el primer punto queda incompleto,

(iii) Especialización de jóvenes investigadores en el estudio del desarrollo larval de los peces en el laboratorio, lo que facilitará el reconocimiento a nivel específico de huevos, larvas y juveniles,

(iv) Establecimiento de programas cooperativos, que si bien contemplen aspectos prioritarios del interés de cada país participante, tiendan a un conocimiento integral del ictioplancton y den simultaneamente la oportunidad de un contacto más directo de jóvenes investigadores con aquellos de mayor experiencia, y asimismo suplan las deficiencias de embarcaciones y equipo o complementen tales necesidades,

(v) Desarrollo de seminarios que abarquen el estudio de familias, géneros y especies de interés (económico, pesquero, deportivo, etc.), pero tratados los más a fondo posible para señalar hechos fundamentales sobre la concentración de adultos, épocas de reproducción y desove, migraciones, caracteres merísticos, etc.,

(vi) Envío de las publicaciones sobre el tema a los especialistas y a las instituciones que la recopilen en cada país,

(vii) Un importante anexo para el desarrollo de las investigaciones podrá ser el servicio que preste el Centro de Preclasificación Oceánica de México (CPOM) en varios aspectos.

- Separación de huevos y larvas de las colecciones de muestras y su preclasificación primaria a nivel de familia, lo que además de facilitar el trabajo del especialista llevaría a un conocimiento integral del grupo y no al estudio de unas cuantas familias,

- Ampliación de la colección de referencia a nivel específico en el mencionado centro que serviría de base a los investigadores del área, a través del envío de material determinado por los especialistas,

- Facilidades para el desarrollo de seminarios,

- Compilación de referencias bibliográficas y elaboración de manuales y altas para familias, géneros y especies.

Bajo esta serie de consideraciones, las investigaciones sobre ictioplancton en el área CICAR podrán cubrir sus objetivos primarios señalados anteriormente en un tiempo más breve y en un área mayor.

5. CONCLUSIONES

Los programas sobre ictioplancton que se desarrollaron en el área y dentro del marco CICAR, incrementaron fuertemente los estudios en este campo de investigación, aunque sólo representaron una fracción muy pequeña dentro de los programas nacionales presentados durante las reuniones del Grupo Internacional de Coordinación CICAR.

Solamente Cuba, EE.UU. y la U.R.S.S. han desarrollado programas de muestreos periódicos que permiten obtener información básica acerca de la abundancia relativa y distribución de la fauna ictioplanctónica en el área CICAR. Jamaica a través de la Universidad de Indias Occidentales ha desarrollado también un programa de muestreo sistemático pero en zona muy restringida.

El equipo de muestreo no ha sido homogéneo a través de todos los programas y países, lo que resta valor comparativo a los trabajos.

El número de investigadores en este campo y para el área CICAR no pueden ser definidos categóricamente por falta de información. No obstante, como se deduce de la información obtenida directa o indirectamente, la mayor parte de los países limítrofes del Caribe, sólo cuentan con una o dos personas, e incluso Cuba tiene únicamente cinco investigadores a nivel universitario (comunicación personal) y en Jamaica, México y otros, la mayor parte son investigadores jóvenes en este campo.

Los aspectos cooperativos estuvieron limitados a los programas cubano-soviéticos, iniciados aún antes de las CICAR y a las visitas de los B/O OREGON II de EE.UU. y AKADEMIK KURCHATOV de la U.R.S.S. a diversos países del área, visitas dentro de las cuales se aprovechó para intercalibración de redes.

Por otro lado el aspecto más fuerte de cooperación se realizó a través del seminario sobre huevos y larvas que se ha venido mencionando en virtud de la información intercambiada y principalmente por el establecimiento de contactos personales entre los investigadores.

Finalmente debe concluirse que la toma de muestras de ictioplancton, la separación y la identificación de huevos y larvas de peces y el análisis subsiguiente de los datos debe continuar, así como cultivos en el laboratorio a fin de tener más y mejor información para la identificación de los primeros estadios de la ictiofauna del área y que esta continuación en virtud de la extensión del mar patrimonial lleva obligadamente a un proceso de estudios cooperativos, bajo el cual las investigaciones futuras en este campo avanzarán más de prisa.

Por último se debe considerar que el futuro de las investigaciones sobre ictioplancton en el área CICAR está condicionado en su crecimiento a los siguientes factores primarios:

(a) embarcaciones adecuadas
(b) equipo adecuado
(c) bibliografía disponible
(d) cooperación internacional
(e) personal capacitado

La falta de personal a nivel universitario sobre este campo en la mayor parte de los países del área constituye la mayor deficiencia. Por tal motivo, la capacitación de personal y establecimiento de programas cooperativos son puntos esenciales para el mayor desarrollo de este campo de investigaciones.

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ANTIBIOSIS IN MARINE SPONGES

by

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CONTENTS

1. INTRODUCTION
2. MATERIAL AND METHODS
3. RESULTS
4. DISCUSSION
5. REFERENCES

Abstract

The results of research conducted on the antibiotic activity of extracts from toxic marine sponges collected in the Gulf of Mexico and on the Pacific Coast of North America in cold temperate, warm temperate and tropical zones are reported. Extracts from 24 species of toxic sponges were obtained with methanol and acetone, separately, by homogenization and centrifugation. A sensitivity test was conducted with Gram-positive and Gram-negative bacteria. Of the 24 species of sponges studied, extracts of 15 demonstrated activity against *Bacillus subtilis* and extracts of 12 demonstrated activity against *Escherichia coli*.

The possible role of antibiotic substances in the life of the sponges as an offensive mechanism in feeding, to inactivate micro-organisms before they are ingested, and as a defensive mechanism through exerting some control of microbial infections, is discussed.

Resumen

Se reportan los resultados de las investigaciones sobre la actividad antibiótica de extractos de esponjas marinas tóxicas colectadas en el Golfo de México y en la costa del Pacífico de Norte América en zonas templado fría, templado cálida y tropical. Extractos de 24 especies de esponjas tóxicas fueron obtenidos con metanol y acetona separadamente por homogeneización y centrifugación. Se siguió un ensayo bacteriológico de determinación de actividad antibiótica en contra de bacterias Gram-positivo y Gram-negativo. De las 24 especies de esponjas estudiadas, extractos de 15 especies mostraron tener actividad contra *Bacillus subtilis* y extractos de 12 especies mostraron tener actividad contra *Escherichia coli*.

Se discute que la posible función que las substancias antibióticas desempeñan en la vida de las esponjas es como mecanismo ofensivo de ayuda en la nutrición, inactivando micro-organismos antes de ser ingeridos, y como mecanismo defensivo, participando en forma importante en el control de infecciones microbianas.

1. INTRODUCTION

During our investigation into the ecology of toxins produced by marine sponges, we became interested in the fact that extracts obtained from sponges contain substances with antibiotic, antitumoral, anticellular and hypotensic activity. In 1959, for example, Nigrelli *et al.* were the first to obtain a broad spectrum antimicrobial agent from a marine sponge. This substance, which was named Ectyonin, was extracted from the sponge *Microciona prolifera* (Ellis and Solander) and demonstrated antimicrobial properties against Gram-positive, Gram-negative and acid-fast bacteria and against the fungus *Candida albicans*.

After a series of experiments, Jakowska and Nigrelli (1960) concluded that the antibiotic substances are produced by the sponge itself and not by the bacteria which live in association with it. In addition, these investigators obtained substances with a variable degree of antimicrobial activity from the following sponges: *Cliona celata* Grant, *Dysidea etheria* De Laubenfels, *Halichondria panicea* (Pallas), *Haliclona viridis* (Duchassaing and Michelotti), *Oligoceras hemorrhages* De Laubenfels and *Tedania ignis* Duchassaing and Michelotti.

In 1961, Ruggieri *et al.* reported extracts from some of the above mentioned sponges to be toxic to fertilized and unfertilized eggs of the sea urchin *Arbacia punctulata*, producing cytolysis and aberrations during cleavage and the formation of larvae.

Baslow and Read (1968) discovered that extracts from the sponges *Haliclona magniculosa* Hechtel, *Haliclona viridis* (Duchassaing and Michelotti) and *Toxadocia violacea* (De Laubenfels) have a hypotensic effect on rats.

Sharma *et al.* (1968, 1970) reported the chemical properties of some antibiotic substances from the sponges *Dysidea herbacea* (Keller), *Homaxinella* sp., *Pellina carbonaria* (Lamarck), *Phakellia flabellata* (Carter), *Plakortis* sp., *Verongia fistularis* (Pallas) and *Verongia cauliformis* (Carter).

In 1969, Baslow and Turlapaty reported that aqueous extracts of *Haliclona viridis* (Duchassaing and Michelotti), when injected intraperitoneally in white mice, prevent growth of Ehrlich ascite tumor cells after a course of treatment initiated four days after tumor innoculation.

Burkholder and Ruetzler (1969) reported their research on the antimicrobial activity a large number of sponges collected from the Caribbean Sea, Mediterranean Sea and Pacific Ocean.

In 1970, Sigel *et al.* reported the results of their work on the anticellular and antitumoral activity of extracts from 104 genera of tropical marine invertebrates. They found that alcohol extracts from the sponges *Chondrilla nucula* Schmidt, *Haliclona substrangularis* (De Laubenfels) and *Ircinia fasciculata* (Pallas) give some protection against the formation of tumors in rats with leukemia P-388.

Stempien *et al.* (1970) reported the results of their research on extracts of sponges collected in Jamaica and the Virgin Islands. Extracts from 23 species have antibiotic activity, extracts from two species produce nuclear anomalies in KB oral carcinoma cells and extracts from four species produce cytoplasmic anomalies in the same type of carcinoma.

In 1973, Andersen and Faulkner reported the results of their investigation on the antibacterial activity of invertebrates of the Gulf of California. The sponges *Verongia thiona* De Laubenfels and *Verongia* sp. produce substances with antibacterial properties.

Based on the results of the above mentioned works, we conducted an investigation on the antibiotic activity of toxic marine sponges against Gram-positive and Gram-negative bacteria to explore the potential biomedical importance of the sponge antibiotics and investigate some of the ecological implications of their role in the life of the Porifera which possess them.

2. MATERIAL AND METHODS

The material for this investigation consisted of 24 species of toxic marine sponges collected in the Gulf of Mexico in the region of Veracruz, on the Pacific Coast of North America at San Juan Island, Washington; Santa Catalina Island, California and Zihuatanejo Bay, Guerrero, Mexico.

The sponge extracts were prepared with fresh and fresh-frozen material using methanol and acetone, separately, as solvents. One-half gramme of sponge and 5 ml of solvent were homogenized and centrifuged. One-half millilitre of supernatant was applied to each sterile filter paper disc 5 mm in diameter, which was allowed to dry at room temperature. Control discs were prepared by impregnating them with solvents only. Commercial antibiotic discs with known concentrations were used only as a guide to measure inhibition zones, since the results of sponge extracts and commercial antibiotics cannot be compared on an equivalent basis. Two flasks containing nutrient agar were innoculated with 24-h cultures of *Bacillus subtilis* and *Escherichia coli* respectively. Twenty millilitres of the innoculated medium were placed in each Petri dish and later the discs were placed in the solidified medium and incubated at 37°C. At 24 and 48 h of incubation the cultures were observed and the inhibition zone around the discs measured.

The commercial antibiotics used were: Chloromycetin (10 mcg), Erythromycin (10 mcg), Neomycin (10 mcg), Penicillin (5 and 10 units), Streptomycin (5 mcg), Terramycin (10 mcg) and Tetracycline (10 mcg) (Table I).

TABLE I

Activity of commercial antibiotics against *Bacillus subtilis* and *Escherichia coli*

Commercial antibiotics and concentration	Zones of inhibition in mm			
	Bacillus subtilis		*Escherichia coli*	
	24-h incubation	48-h incubation	24-h incubation	48-h incubation
Chloromycetin, 10 mcg	5	5	5	5
Erythromycin, 10 mcg	5	6	0	0
Neomycin, 10 mcg	2	2	1.5	2
Pencillin, 5 units	2	2	1	1
Pencillin, 10 units	3	3	2.5	2.5
Streptomycin, 5 mcg	9	10	4.5	5
Terramycin, 10 mcg	9	10	7	7
Tetracycline, 10 mcg	9.5	10.5	7.5	8

3. RESULTS

These are presented in Tables II and III. Of the 24 species of sponges used to determine their antibiotic activity, extracts from 15 species proved to be active against *Bacillus subtilis*. Of these, five were highly active with zones of inhibition greater than 7 mm. One of these, species V41 *Haliclona* sp., showed extraordinary activity with a zone of inhibition of 19 mm. The commercial antibiotic most active against *Bacillus subtilis* proved to be Tetracycline (10 mcg), with a zone of inhibition of 10.5 mm.

TABLE II

Activity of extracts from toxic sponges against *Bacillus subtilis*

Sponge Code Number	Sponge species	Zones of bacterial inhibition in mm			
		24-h incubation		48-h incubation	
		Methanol	Acetone	Methanol	Acetone
FH5	*Halichondria panicea* (Pallas)	0	0	0	0
FH37	*Mycale lingua* (Bowerbank)	4	4	4.5	4.5
SC4	Unidentified sponge	0	0	0	0
SC7	*Isociona lithophoenix* (De Laubenfels)	0	0	0	0
SC10	Dendroceratida	1	3	1.5	3
SC11	*Sigmadocia* sp.	1.5	2	2	2
SC15	Unidentified sponge	0	0	0	0
SC17	*Microciona parthena* De Laubenfels	0	0	0	0
SC27	*Haliclona* sp	8	8	8	8
SC52	Unidentified sponge	6	8	6	8.5
SC60	*Haliclona* sp.	6.5	7.5	7	8
Z1	*Haliclona* sp.	6	7.5	6.5	8
V1	*Haliclona rubens* (Pallas)	2	3	2	3
V5	*Thalyseurypon* sp.	0	0	0	0
V6	*Ianthella* sp.	1	3	1	3
V10	*Haliclona viridis* (Duchassaing and Michelotti)	0.5	1	0.5	1
V11	*Halichondria* sp.	4.5	4	4.5	4
V16	*Haliclona* sp.	2	2	2	2
V17	*Chondrilla nucula* Schmidt	0	0	0	0
V22	*Haliclona* sp.	0	0	0	0
V23	*Adocia* sp.	0	0	0	0
V24	*Ircinia fasciculata* (Pallas)	2	1	2	1
V37	Myxillidae	2	3	2	3
V41	*Haliclona* sp.	8	12	8	19
-	Control	0	0	0	0

TABLE III

Activity of extracts from toxic sponges against *Escherichia coli*

Sponge Code Number	Sponge species	Zones of bacterial inhibition in mm			
		24-h incubation		48-h incubation	
		Methanol	Acetone	Methanol	Acetone
FH5	*Halichondria panicea* (Pallas)	0	0	0	0
FH37	*Mycale lingua* (Bowerbank)	3	3	3	3.5
SC4	Unidentified sponge	0	0	0	0
SC7	*Isociona lithophoenix* (De Laubenfels)	0	0	0	0
SC10	Dendroceratida	0	0	0	0
SC11	*Sigmadocia* sp.	0	0	0	0
SC15	Unidentified sponge	0	0	0	0
SC17	*Microciona parthena* De Laubenfels	0	0	0	0
SC27	*Haliclona* sp.	3.5	4	3.5	4
SC52	Unidentified sponge	3	4	3.5	4
SC60	*Haliclona* sp.	3	3	3	3
Z1	*Haliclona* sp.	0.5	1.5	0.5	1.5
V1	*Haliclona rubens* (Pallas)	1	1	1	1
V5	*Thalyseurypon* sp.	0	0	0	0
V6	*Ianthella* sp.	0	0	0	0
V10	*Haliclona viridis* (Duchassaing and Michelotti)	0	0	0	0
V11	*Halichondria* sp.	0.5	1	0.5	1
V16	*Haliclona* sp.	1	0.5	1	0.5
V17	*Chondrilla nucula* Schmidt	-	0	-	0
V22	*Haliclona* sp.	0	0	0	0
V23	*Adocia* sp.	1	0	1	0
V24	*Ircinia fasciculata* (Pallas)	0.5	1	0.5	1.5
V37	Myxillidae	2	3	2	3
V41	*Haliclona* sp.	4	6	4.5	6
-	Control	0	0	0	0

Extracts of 12 species proved to be active against Escherichia coli. Of these only one, again species V41 Haliclona sp., showed a high degree of activity, with a zone of inhibition of 6 mm. The commercial antibiotic most active against Escherichia coli was Tetracycline (10 mcg) with a zone of inhibition of 8 mm.

4. DISCUSSION

Based on information in the literature and on our observations and experiments, it is possible that the sponges which produce antibiotics use them as offensive and defensive mechanisms.

As an offensive mechanism, the antibiotics are possibly used as inactivators of microbial prey prior to their phagocytosis and digestion (Burkholder, 1973). In support of this, Di Salvo (1971, 1973), Reiswig (1971) and Sorokin (1971, 1973), found that marine bacteria are a very important source of food for sponges in tropical waters. In addition, Madri et al. (1967) and Claus et al. (1967) reported that Microciona prolifera (Ellis and Solander) very efficiently filters the bacteria Escherichia coli and Cryptococcus neoformans and the fungus Candida albicans from contaminated waters, concentrating and digesting them. The possibility of using this sponge to combat microbial contamination produced by faecal waste in estuaries has, in fact, been suggested. It should be noted again that Nigrelli et al. (1959) obtained a broad spectrum antimicrobial substance (Ectyonin) from this same sponge.

As a defensive mechanism it is possible that sponge antibiotics are an important aid in the fight against microbial infections. Sponges, like most organisms, are vulnerable to such infections. This vulnerability is even greater since they have filter feeding and sessile habits. The disease of the commercial sponges of the Caribbean Sea and the Gulf of Mexico which, at different times, has caused great losses for the sponge industry is well known (Smith, 1941; Galtsoff, 1942; Osorio and Cardenas, 1945; Storr, 1964). However, sponges have the ability to fight microbial infections by isolation and elimination of the affected part (Connes, 1967; Cheng et al., 1968). In this process the activity of antibiotic substances might play an important role.

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REPORT OF
COLLOQUIUM ON SNAPPER AND GROUPER FISHERY RESOURCES OF THE WESTERN CENTRAL ATLANTIC OCEAN

by

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CONTENTS

1. INTRODUCTION
2. THE RESOURCE
3. THE FISHERY
4. BIOLOGICAL RESEARCH
5. ECONOMICS
6. INDUSTRY PROBLEMS
7. SUGGESTED SOLUTIONS
8. REFERENCE

Abstract

A Colloquium on snapper and grouper fishery resources was held at the October 1975 meeting of the Gulf States Marine Fisheries Commission (GSMFC). Information on the resource and fishery was presented and problems and possible solutions were discussed. Proceedings of the Colloquium will be available from GSMFC, 531 St. Louis Street, New Orleans, Louisiana 70130.

The colloquium technique is recommended as a mechanism for management agencies to obtain information and advice from all concerned groups and, used in this way, is an effective tool in the planning process.

Problems of the snapper and grouper fisheries include increased competition between commercial, recreational and foreign fisheries, greater fishing pressure on the resource, and decreasing margins between income and costs of operation. Solutions to these problems will come from management action based on reliable statistical and biological information.

Resumen

En la reunión de octubre de 1975 de la Comisión de Pesca Marítima de los Estados del Golfo (GSMFC) tuvo lugar un coloquio sobre los recursos de pargo y mero (cherna), en el que se presentó información sobre esos recursos y sus pesquerías y se examinaron los problemas planteados y sus posibles soluciones. Las actas del coloquio pueden pedirse a GSMFC, 531 St. Louis Street, New Orleans, Louisiana 70130.

Para los organismos responsables de la ordenación pesquera, los coloquios constituyen un mecanismo útil para obtener información y asesoramiento de todos los grupos interesados. Así utilizada, esta técnica constituye un instrumento eficaz en el proceso de planificación.

Entre los problemas de las pesquerías de pargo y mero pueden citarse: creciente competencia entre la pesca comercial, la pesca deportiva y las actividades extranjeras; aumento de la presión a que está sometidos los recursos; y reducción de los márgenes entre los beneficios y los costos de explotación. Para resolver esos problemas será necesario ordenar la explotación, basándose en información biológica y estadísticas fidedignas.

1. INTRODUCTION

In October 1975 the Gulf States Marine Fisheries Commission - an interstate compact commission including Texas, Louisiana, Mississippi, Alabama and Florida - sponsored a Colloquium in Pensacola, Florida on the snapper and grouper fishery resources of the western central Atlantic Ocean. I will present a report of this Colloquium, both to suggest a method of procedure in fishery management and to summarize the present knowledge of this resource and its fishery.

Over 30 species of snappers and groupers are important components of reef fish communities in the tropical and sub-tropical western Atlantic Ocean. Reef fish are the basis of important commercial, recreational and subsistence fisheries, and are of primary interest to people in this part of the world.

Important changes have taken place in these fisheries in recent years. Subsistence fisheries have been replaced by industrial fisheries as technological development has proceeded. Commercial fisheries dating back over 100 years have fluctuated in success and shifted in area. Recreational fisheries - a relatively new development - have expanded. What do these changes mean to fishery management? How do we define the critical management problems and take effective action?

The Southeast Fisheries Center, a research unit of the National Marine Fisheries Service, has been concerned with the U.S. snapper-grouper fishery. In particular, we were seeking explanations for the decline in total snapper and grouper landings by the U.S. commercial fishery over the past decade. When our preliminary results were presented, the Gulf States Marine Fisheries Commission suggested the subject be addressed in Colloquium format. We contacted individuals through letters and news releases, inviting them to attend and participate in a Colloquium. The aim was to involve concerned people in problem definition and solution formulation.

The Colloquium was designed to accomplish three objectives. First, to assemble available information concerning the resource and the fishery. Second, to define economic problems of the industry and management requirements for the fishery. Third, to suggest solutions that could form the basis of decisions by an appropriate management group or agency.

These objectives, perhaps, do not sound unique or innovative. For years, fishery management agencies have done research, dealt with problems and made decisions. Management decision-making has formed the basis of numerous textbooks and research papers in the business world. What, perhaps, is unique, is that we tried to draw together a particularly diverse group of people, involved each in his particular expert capacity, deal with a single resource problem and conclude with specific recommendations. A fourth, and final, objective - action - was outside the authority of the Colloquium.

Fishery management has undergone a number of changes over the last decade - a trend toward greater use of quantitative data in decision-making, consideration of economic and social as well as biological factors and the need to make rapid decisions, with the corollary that decisions must often be made with limited data. It is this last feature - decision-making with limited data - which was of particular concern.

The snapper-grouper resource, although of great importance to the fisheries of many areas, has received relatively little attention. It is important to define the problems of utilizing this resource and to assemble the information that will be most useful in dealing with these problems.

The Colloquium was composed of three panels. These panels dealt with:

1. The Information and Technical Data Base;
2. The Definition of Industry Problems; and
3. The Development of Solutions.

We asked three groups of people to participate in the panels. Panel 1 consisted of technical people. Review papers were prepared on specialized topics:

1. The Resource;
2. The Commercial Fishery;
3. The Recreational Fishery;
4. The Biological Knowledge Necessary for Management; and
5. The Economics of the Industry.

In addition, contributed papers were prepared on specialized topics. Some of these topics included the snapper fishing banks off Texas, the party-boat fishery of the Carolinas, the use of traps to catch snapper and the geographical and depth distribution of various species.

Discussion of these review and contributed papers provided an information base, documented historical changes that had taken place and suggested possible management problems of the resource and the fishery.

Panel 2 consisted of users of the resource; commercial fishermen, charter-boat operators (who might be classed as commercial-recreational fishermen) and wholesale seafood dealers. These had intimate knowledge of industry problems and day-to-day acquaintance with the fishery, since all gained their livelihood from the resource. Each described the problems of the industry as perceived from his particular viewpoint. Agreement was reached on major problems.

Panel 3 consisted of state and federal fishery administrators. Their task was to consider the problems defined by panels 1 and 2 and suggest a course of effective action.

The papers and discussions will be published by the Gulf States Marine Fisheries Commission; they document the problems and provide reference material to those involved in management of this resource. The following sections of this paper will briefly summarize the proceedings.

2. THE RESOURCE

Red snapper (*Lutjanus campechanus*) and red grouper (*Epinephelus morio*) are targets of present intensive fisheries. Nevertheless, increases in yield of these species can be gained by proper management. Other species of snapper and grouper are less intensively fished and, generally, have potential for increased yield.

3. THE FISHERY

Substantial changes have taken place in the U.S. fishery in recent years. In some areas fishermen have transferred from commercial fishing to commercial-recreational fishing, indicative of a shift in the economics of exploitation. In many localities the recreational fishery has grown to be larger than the commercial fishery. Since 1949, the size of the commercial fleet first increased, and then declined. The peak number of boats, 3 290 of less than 5 net tons (4.5 metric tons), was reached in 1956 and the peak number of vessels, 546 of more than 5 net tons, was reached in 1959. In contrast, there are probably 1 million recreational craft in the South Atlantic and Gulf States and groupers and snappers are among the primary species sought by the operators of these craft.

Commercial landings in the United States peaked at 26 million pounds (11 794 metric tons) in 1965 and then declined to 18 million pounds (8 165 metric tons) in 1974. Recreational landings were 83 million pounds (37 649 metric tons) in 1970 and appear to be still growing.

Regarding snapper, catches off the U.S. coast have been level and U.S. catches off Mexico and the Caribbean have declined. Regarding grouper, catches off the U.S. coast have fluctuated and it is not clear whether or not there is a significant decline; U.S. catches off Mexico and in the Caribbean have declined. The U.S. distant-water fisheries face increasing competition from local fleets and find it difficult to operate profitably at lower levels of stock abundance.

4. BIOLOGICAL RESEARCH

It was suggested that fishery biologists had been generally neglectful in gathering sufficient biological information to manage the resource adequately. However, there have been outstanding scientific studies of the red grouper (*Epinephelus morio*), the gray snapper (*Lutjanus griseus*) and the red snapper (*Lutjanus campechanus*). We can answer some basic fishery management questions for these species from data presented at the Colloquium.

1. How long do the fish live, how fast do they grow and what age classes are vulnerable to the fisheries? The fish are generally long-lived and slow-growing. Red snapper live at least ten years and red grouper 17 years.

2. When do the fish become sexually mature? Red snapper may mature within one year. Red grouper are protogynous hermaphrodites, changing to males between ages five and ten.

3. Where, when and how often do they spawn? Red grouper spawn once per year, principally in April and May, offshore in 24-47 m. Red snapper may spawn several times per year, principally from July through September, offshore, in 18 or more m.

4. Where are the larvae and juveniles distributed relative to the fishery? Specifically, do they require critical ecological niches? Little is known of the distribution, or even description, of snapper or grouper larvae. Small grouper and snapper inhabit nearshore reefs or smooth bottom and move to deeper water as they grow older. Small snapper inhabit areas of sea bed which are regularly trawled for shrimp, and small grouper inhabit the nearshore reefs which are the main location of the small boat recreational fishery.

It was pointed out that long-lived, slow-growing fish are especially susceptible to population reduction through fishing pressure. Constant and intensive removal of newly recruited year classes may seriously reduce the numbers of spawners necessary to maintain a high level of recruitment.

5. What are the mortality rates, the population dynamics, stock structure and potential yields? Answers to these questions were not available, but interest was stimulated to begin such studies.

5. ECONOMICS

The State of Florida dominates the U.S. commercial industry. Eighty percent of snapper landings are made in Florida and Florida prices, which fluctuate with supply of fish, control prices in other areas. A commercial boat can land between 80 000 and 130 000 pounds (36 and 59 metric tons) of snapper and grouper per year, depending on its size. A commercial recreational party boat lands an equivalent amount of about 20 pounds (9.1 kg) per fisherman, based on an average of 6 700 fishermen per year per boat.

6. INDUSTRY PROBLEMS

Some problems identified include:

1. Low commercial landings. In part, low commercial landings reflect growth of the recreational fishery, for which statistics are incomplete. Some commercial fishermen stated they now have to go farther, and stay longer, to make economically successful trips, because of competition from nearshore recreational fishermen.

2. Competition from foreign fishermen, e.g., the Cuban handline fleet that fishes grouper on the west coast of Florida. It was stated that accommodation of foreign fleets fishing domestic stocks will require a more complete understanding of both the productivity of the resource and the economics of the different fisheries.

3. Smaller size of fish. Fishing intensity on nearshore components of the population is growing and, as a result, the average size of fish caught is smaller. The resource seems to be in no immediate danger of depletion. Construction of artificial habitats might make presently unproductive areas productive, and the introduction of fish-saving gear for shrimp trawls might reduce the mortality of young snapper, thus increasing the available yield. It is believed by some that shrimp trawling destroys bottom suitable for snapper.

4. High operating costs. Initial cost of larger vessels, insurance costs, unavailability of trained captains and skilled, hard-working fishermen, and the necessity of paying sales taxes on ice, fuel and bait, even though fishermen are wholesale operators.

5. Competition from imports, which sell at a lower price than domestic products.

6. Lack of research on such basic questions as why fish bite a hook, which could lead to increased fishing efficiency.

7. Lack of understanding by government agencies. Mention was made of the economic hardship caused by changes in regulations concerning loran and radio communications.

7. SUGGESTED SOLUTIONS

1. Fishery administrators stated that many problems discussed at the Colloquium were technical, and could be solved if adequate financial resources were available.

2. A second suggestion was that responsibility for management should be designated to a single management group. Although the resource lies largely outside state waters, the federal government has limited powers of regulation. Whatever management group is designated, this group will need to be given adequate authority.

3. A third suggestion was that the Gulf States Marine Fisheries Commission should participate in the development of a management policy that represents, or at least considers, the viewpoint of all users.

4. A fourth suggestion was that decisions for management of the resource need to be made and that the time for decision is now.

8. REFERENCE

Bullis, H.R. Jr. and A.C. Jones, Proceedings: colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean. New Orleans, La., Gulf States Marine Fisheries Commission, (in press)

SHRIMP BYCATCH INVESTIGATION IN THE UNITED STATES OF AMERICA
A STATUS REPORT

by

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Abstract

Shrimp have supported the most valuable fishery in the United States of America for many years. Although the fishery for the cold-water species Crangon and Pandalus has increased in recent years in the New England and Alaska areas, the mainstay is still the penaeid shrimp of the southeastern United States. Three species make up the bulk of the catch, Penaeus aztecus, P. duorarum and P. setiferus. The centre of this fishery is in the Gulf of Mexico and along the southeastern seaboard of the United States. The average annual catch of penaeids over the past 25 years has been close to 100 000 t in those areas. Production in recent years from other countries in the CICAR area, including Brazil, has been 70 000 t; worldwide the total annual catch is close to 700 000 t. Minor periodic annual variations in production have occurred, attributed generally to adverse environmental or economic factors. Although the shrimp bycatch problem was long known in the United States; it was not until late 1972 that a project was implemented to study the situation. Basic information was needed for management purposes, for possible use of bycatch and for application to design of gear which would reduce the catch of fish (savings gear), e.g., electric or separator trawls. In view of the relevance of the bycatch problem to other nations in the CICAR area, a description of the ongoing work and preliminary results are presented.

Resumen

Durante muchos años, los camarones han dado vida a la pesquería más valiosa de los Estados Unidos de América. Aunque la explotación de las especies de agua fría Crangon y Pandalus ha aumentado en los últimos años en las zonas de Nueva Inglaterra y Alaska, los recursos principales siguen siendo los camarones peneidos del sudeste de los Estados Unidos. El grueso de las capturas pertenece a tres especies: Penaeus aztecus, P. duorarum y P. setiferus. El centro de esta pesquería se encuentra en el Golfo de México y a lo largo de la costa sudoriental de los Estados Unidos. En esas zonas, la captura anual media de peneidos durante los últimos 25 años se ha acercado a las 100 000 t. La producción de otros países de la zona de las ICCRA, incluido el Brasil, ha sido de 70 000 t; la captura mundial total asciende anualmente a unas 700 000 t. Se han registrado variaciones periódicas anuales

de poca importancia en la producción, atribuidas en general a factores ambientales o económicos adversos. Aunque el problema de las capturas accidentales de otras especies en la pesquería de camarón se conocía hace tiempo en los Estados Unidos, sólo a finales de 1972 se llevó a cabo un proyecto para estudiar la situación. Era necesario disponer de información básica para regular la explotación, ver las posibles maneras de aprovechar esas capturas accidentales y modificar el diseño de los artes con vistas a reducir las capturas de peces de escama, por ejemplo introduciendo equipo eléctrico o redes de arastre separadoras. Dado que el problema de las capturas accidentales afecta también a otros países de la zona de las ICCRA, el presente trabajo ofrece una descripción de los trabajos en curso y de los primeros resultados obtenidos.

1. INTRODUCTION

The shrimp industry is the most important fishery in the United States in value and ranks third in volume. Present annual landings total over 150 000 t (heads-on weight). The principal species comprising the commercial landings include the two cold-water genera Crangon and Pandalus, taken off New England and Alaska. The most important, however, is the genus Penaeus from the Gulf of Mexico and southeastern United States. The fishery for this group will be the subject of this paper, especially in relation to the bycatch, which is the collective name given to fish and other animals taken incidentally to the shrimp catch.

Many trawl fisheries are not completely selective, large numbers of animals being taken incidentally to the target species. Often, most of this incidental catch is discarded. Although the shrimp industry centres essentially within the United States' coastal areas, the incidental or bycatch problem is of importance in many fisheries of the Atlantic Ocean as well as other areas of the world. Examples include the Geryon and Nephrops fishery in the northeastern Atlantic, where juvenile gadoids such as hake and whiting are taken as bycatch and discarded. In the northwestern Atlantic, 40 percent to 70 percent of the trawl catches may be discarded, including undersized fish or species of low market value as well as any excess of species taken under International Commission for Northwest Atlantic Fisheries (ICNAF) quotas. Another example, in the Gulf of Mexico, is trawling for large croaker (Micropogon sp.) for human consumption. Approximately 40 percent to 50 percent of the catch (small fish) is discarded (Juhl, 1974). In the Caribbean, in addition to the shrimp fishery, the fish pot and beach seine fisheries are also noted for their bycatch problem. (All values in heads-on weight.)

2. BACKGROUND

The penaeid shrimp fishery bycatch problem is undoubtedly worldwide; this is due to the similarity of fauna existing in the areas where penaeids are taken and the similarity of the fishing gear. According to FAO fishery statistics, the total world catch of penaeid shrimp in the past several years has been over 700 000 t (Ivanov, 1971). Applying a conservative ratio of 5:1 of fish to shrimp, the magnitude of the bycatch can be appreciated. Regarding other shrimp-producing countries in the western central Atlantic region, including the Gulf of Mexico and Caribbean, but excluding the United States, the total annual catch of penaeids in the last three to four years was about 70 000 t (FAO, 1973). Applying the fish to shrimp ratio of 5:1, it can be assumed that at least 350 000 t of fish were discarded annually.

In the United States, with regard to the bycatch, basic information on extent, composition, size, distribution, seasonal changes and environmental effects is spotty or non-existent. Since statistics are normally collected from port landings or processing plants and not at sea, problems of collecting pertinent data are obvious. The need for these data, however, is urgent not only to provide knowledge to determine if savings gear would be effective or to consider the utilization of the bycatch, but also to calculate maximum sustainable yield (MSY) or optimum sustainable yield (OSY) of the stocks for management purposes.

The recent controversy between the application of these two concepts can be readily appreciated. MSY for one species (shrimp) where an unknown but large portion of the catch is discarded is certainly questionable as to its rational validity. OSY would take other factors into account including social and economic impacts; however, relevant details on the extent of the bycatch is essential to arrive at meaningful analyses and conclusions. Such information also provides essential input for resource assessment of interrelated fisheries.

The importance of the bycatch issue was noted several years ago in earlier independent and unrelated projects. However, it was not until the end of 1972 that a formal project, Shrimp Fleet Discard Survey, was instituted as part of a programme drafted to evaluate the groundfish (demersal) resources of the northern Gulf of Mexico. This programme, Oceanic Resources Surveys and Assessment, is under the direction of the Pascagoula Fisheries Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, U.S. Department of Commerce. The Shrimp Fleet Discard Survey Project is concerned with collecting bycatch data from the shrimp fleet and other sources such as published fishery statistics, state agencies and research institutions. The main area of activity is the Gulf of Mexico, from southwest Florida to the Gulf of Campeche, and from the estuarine areas out to 50 fath.

The importance of the shrimp fleet bycatch issue in the southeastern region of the United States, especially the Gulf of Mexico, can be gauged by the number of vessels engaged in the fishery. At present, an estimated total of 3 750 trawlers of over 5 net tons operate in offshore waters (deeper than 3 fath) and from 18 000 to 20 000 boats (not including recreational fishing boats) under 5 net tons may operate in inshore waters of this region. A general view of the production trend is illustrated in Fig. 1, which shows the total annual landings of penaeid shrimp in the United States from 1950 to 1974. The average landing for this period was nearly 100 000 t (heads-on). Between 1950 and 1970 the number of shrimp vessels (over 5 net tons) increased from 3 000 to nearly 4 000; since 1970, numbers have decreased. The gross tonnage of all vessels, however, rose from 118 000 in 1960 to over 198 000 in 1970 (Whitaker, 1973). This is almost a 70 percent increase in fishing power, yet the total shrimp catch has remained nearly unchanged (Nichols and Griffin, 1975). The relevance of this to the bycatch problem rests on two main assumptions. First, the increase in fishing power implies greater fishing effort and a consequent increase in bycatch. An increase in bycatch is assumed because historical catch records for the fish trawl fleet operating in the same area do not indicate a diminishing catch per unit of effort, but a slight increase (Juhl, 1974; Roithmayr, 1965). Second, due to limitations in fishing activity

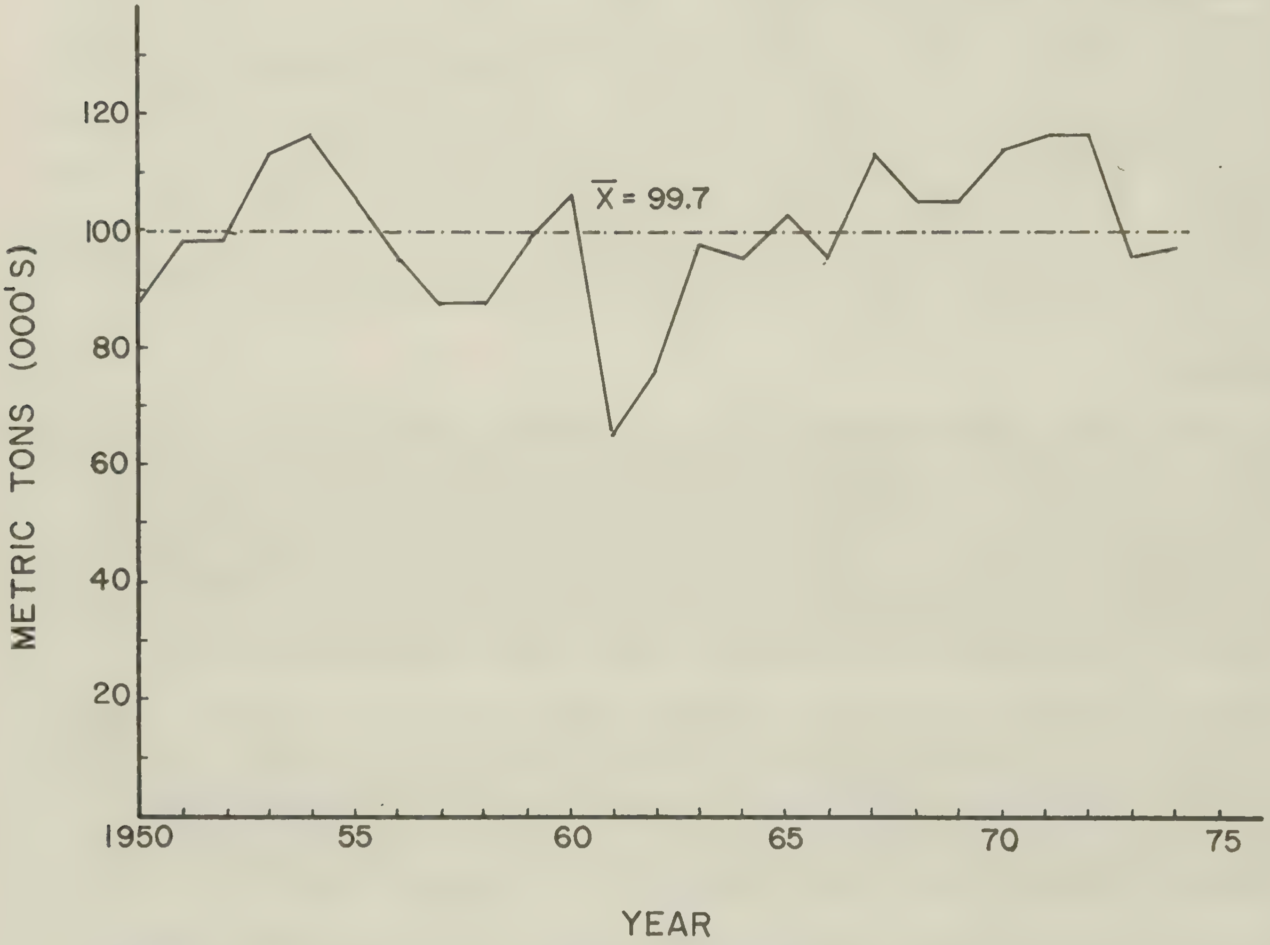

Fig. 1 U.S. penaeid shrimp landings, Gulf of Mexico and southeastern seaboard (adapted from Whitaker, 1973 and Surdi and Hutchinson, 1975)

because of the larger fishing fleet operating within limited boundaries, and higher prices paid for shrimp, which compensate for lower catch rates, the vessels have extended their operations. The extension has been into areas where the proportion of fish catch is relatively greater than on traditional fishing grounds. It is probable that these factors have a direct relevance to other shrimp fishing areas in the CICAR region in that the same pattern will develop as the fishery continues to develop.

Three species make up the bulk of the shrimp catch, Penaeus aztecus (55 percent), P. duorarum (23 percent) and P. setiferus (20 percent). Areas of greatest fishing effort enter in the north central Gulf and the Tortugas grounds, southwest of Florida (Fig. 2).

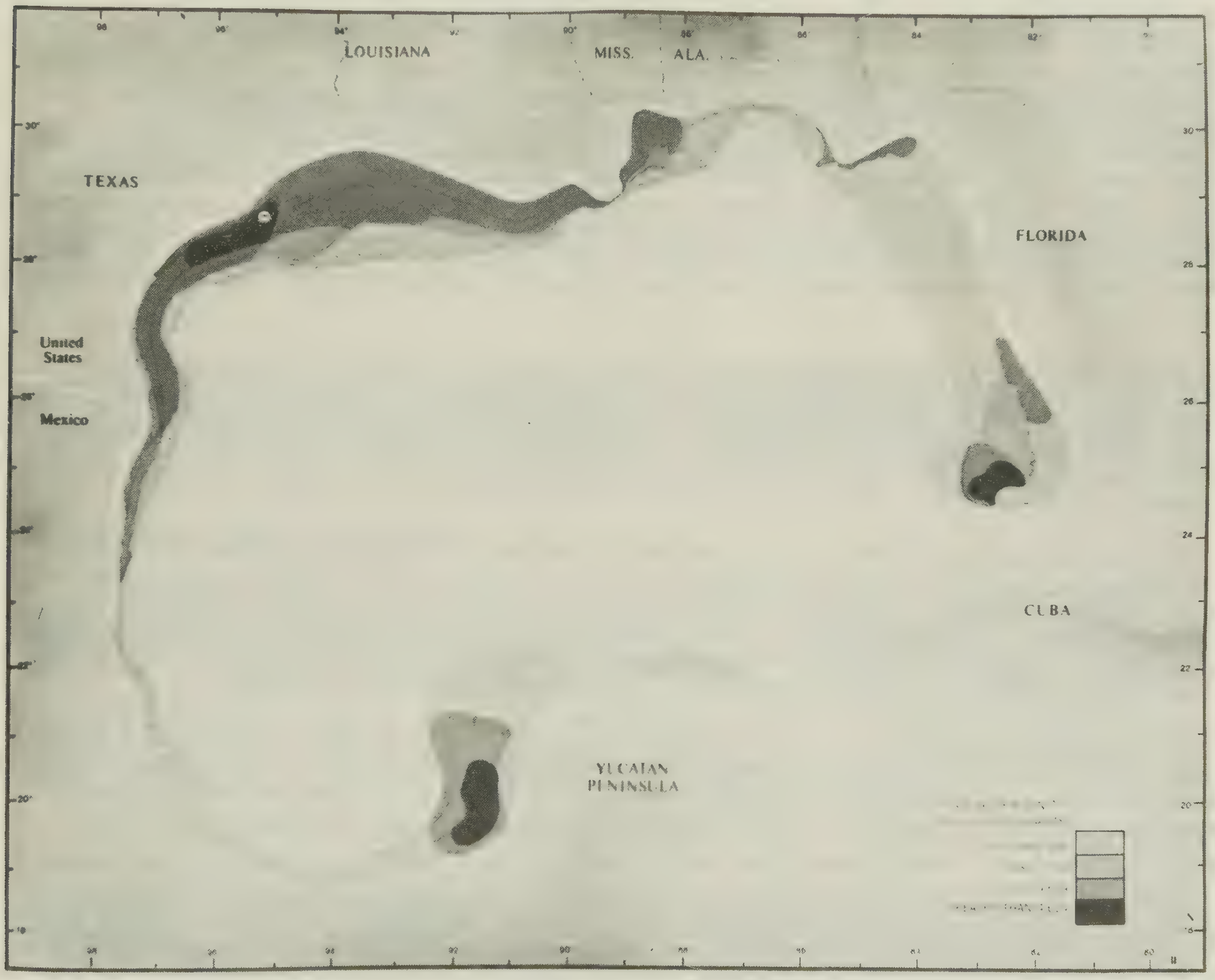

Fig. 2 Gulf of Mexico shrimp grounds

Preliminary data collected by the aforementioned Shrimp Fleet Discard Survey Project indicate the annual volume of fish discarded by the Gulf of Mexico fleet could reach 1 million t. This was based, in part, on the ratio of shrimp to fish taken by trawling. The ratio of shrimp to fish had been estimated at 1:10; hence, 100 000 t x 10 = 1 million t. This ratio was, and is still, considered a rough estimate and the need for verification is evident. Problems associated with the shrimp bycatch other than its possible use are not so apparent, but are noteworthy. For example, capture of incidental fish by the shrimper increases labour cost in sorting; finfish discarded are lost to other trawl fisheries; discards in estuarine and inshore areas could create accumulations of dead fish and cause environmental deterioration; last, but not least, the loss of potential protein from the world food supply is tremendous.

The portion of the bycatch returned to the sea alive is very small, consisting mostly of crustaceans (Callinectes and Portunus), molluscs and gastropods not wanted owing to their low market value. The duration of a complete trawling operation is from two to four hours; many organisms, especially fish, die from suffocation during this period. The change in hydrostatic pressure created by hauling the trawl to the surface and lifting the codend on to the deck may also cause irreparable damage.

Sorting shrimp from the catch can take from 15 to 30 min, depending on volume. Few fish survive that long out of water and those that remain alive are shoveled overboard where they are attacked by numerous predators.

The possibility of making effective use of the bycatch has received attention, but the normal operating procedure of the offshore shrimp vessels precludes much flexibility. A typical vessel, 20-22 m LOA, has a hold capacity of 64-85 t. The duration of an average fishing trip is 14 days, including running time to and from port. Shrimp trawling in offshore waters usually takes place only at night. During fishing in areas distant from home port, the catch may be trans-shipped to a carrier vessel, while the fishing boat stays on the grounds. On a trip a vessel carries 35-40 tons of crushed ice, which occupies the greater part of the hold capacity. After each tow the codends are emptied on deck and the shrimp culled from the catch. The bycatch is discarded overboard and the shrimp are beheaded, covered with ice and stored in the hold. Marketable fish, such as snapper and flounder, are also kept. When the shrimp catch is relatively high, culling, beheading, sorting and storing occupies most of the working hours of the crew, making it extremely difficult to process the bycatch also.

Other factors to be considered include insufficient refrigerated storage space, low market price of the bycatch species relative to the much higher price paid for shrimp, lack of sufficient manpower to handle storage of the catch and the human factor - reluctance to change. Therefore, potential utilization of the bycatch would entail concerted studies of present technology and possible alternatives to determine the most rational and economical approach.

Studies are needed on how to hold the bycatch aboard in an acceptable condition, on quick unloading, e.g., by fish pump either at sea or in port, how to hold a maximum amount of fish and how to handle transfer of the fish to a carrier vessel and/or fish processing vessel economically. As a corollary, the problems must be solved relative to the distance from the fishing grounds to the nearest shore processing station or unloading dock, and the minimum number of fishing vessels required to operate effectively in concert.

The possibility of processing the bycatch into meal, or a related product, aboard the larger vessels should also be considered. It must be determined what is the minimum amount of fish that can be processed economically taking into account the cost of the fish meal processing equipment, its installation, additional fuel needs, manpower and reduced fish holding space.

From the foregoing discussion, it is evident that additional knowledge must be gained about the bycatch problem before effective action can be considered. In the following pages the status of the previously mentioned Shrimp Fleet Bycatch Project will be presented. Details of the planning and implementation of the project will also be reviewed, in view of their direct relevance to the developing shrimp and fish trawling industries in many of the nations within the CICAR area.

3. SHRIMP FLEET BYCATCH SURVEY STATUS

Since previous studies have indicated a very large shrimp bycatch, a thorough study of it is essential for purposes of groundfish population assessment and possible industry utilization. The Survey attempts to estimate the bycatch volume in the hope of stimulating and promoting further studies into possibilities of bycatch utilization, and providing management data.

The initial Shrimp Fleet Bycatch Survey plan called for support contracts with Gulf coast states; this approach was postponed until funds were made available in 1976. An alternative approach, however, was then implemented and is still ongoing. Primarily, this approach consists of groundfish surveys along the northern Gulf by the federal research vessels OREGON II and GEORGE M. BOWERS. In addition, the alternative approach takes advantage of related activities conducted by state departments, academic communities and shrimp fishermen willing to provide information or the use of their vessels as sampling platforms for Project personnel. Thus far, all the above sources have contributed significantly to the bycatch data bank.

Though discard data returns are at the scheduled level, the present coverage is not sufficient for a reliable quantitative assessment. Slow data retrieval, uneven reporting time, poor data continuity and consistency and, generally, a lack of central control have all hindered work.

We have calculated preliminary bycatch estimates for certain areas of the Gulf of Mexico. These estimates reflect those data on record and consequently the interpretation and results are subject to change and refinement as sampling improves.

As the investigation continues, a set of reliable data should be assembled. This information base will help to answer questions about resource magnitude, fishery management, and utilization.

4. SURVEY AREA

This includes all U.S. Gulf of Mexico shrimp fishing zones (Fig. 3). Inland bays and lakes are not shown but are considered. For this interim report shrimp landing zones are grouped under four Gulf divisions; Northeastern, Northcentral, Northwestern and Inland Louisiana. Inland Louisiana is separated due to its vast marsh area where shrimp fishing is done. One can associate these areas and zones in Table I under "Locality".

5. DATA ACQUISITION AND TREATMENT

The sampling procedure for shrimp bycatch employs both direct and indirect sampling methods. Direct sampling is sampling the actual catch of commercial shrimp vessels. Indirect sampling is conducted from a research vessel in an area where commercial shrimp fishing vessels are operating, or have operated during the month. The indirect method considers only those samples containing 1.5 kg or more of heads-on shrimp captured per 10 min of trawling time using a 40-ft shrimp trawl. This catch per unit of effort is considered commercially significant. To date, a substantial amount of the data collected has come from the indirect method, but most of the future sampling will be direct.

As samples are taken, data are recorded on discard station sheets (Fig. 4) designed for automatic data processing. These data are transferred onto punch cards. Each station sheet is numbered sequentially and catalogued according to a statistical reporting zone. These zones coincide with the National Marine Fisheries Service's Gulf shrimp landing statistics, which are reported by zone, depth and area (Fig. 3). Data are catalogued in this manner to ensure a correspondence between shrimp landings and fish to shrimp ratios calculated from each survey sample. These ratios, coupled with shrimp landings, are the basis for shrimp bycatch estimates. Simply stated, these ratios are multiplied by the actual shrimp landings.

Another aspect of the Survey considers the bycatch species composition. Each species within a sample is recorded by number and weight. Individual species are then ranked by total weight percentage. Also extracted from this information are the dominant bycatch species for a given area.

Sources of sample data have included the Texas Parks and Wildlife Service, Louisiana Wild Life and Fisheries Commission, shrimp fishermen and surveys conducted by the research vessels OREGON II and GEORGE M. BOWERS.

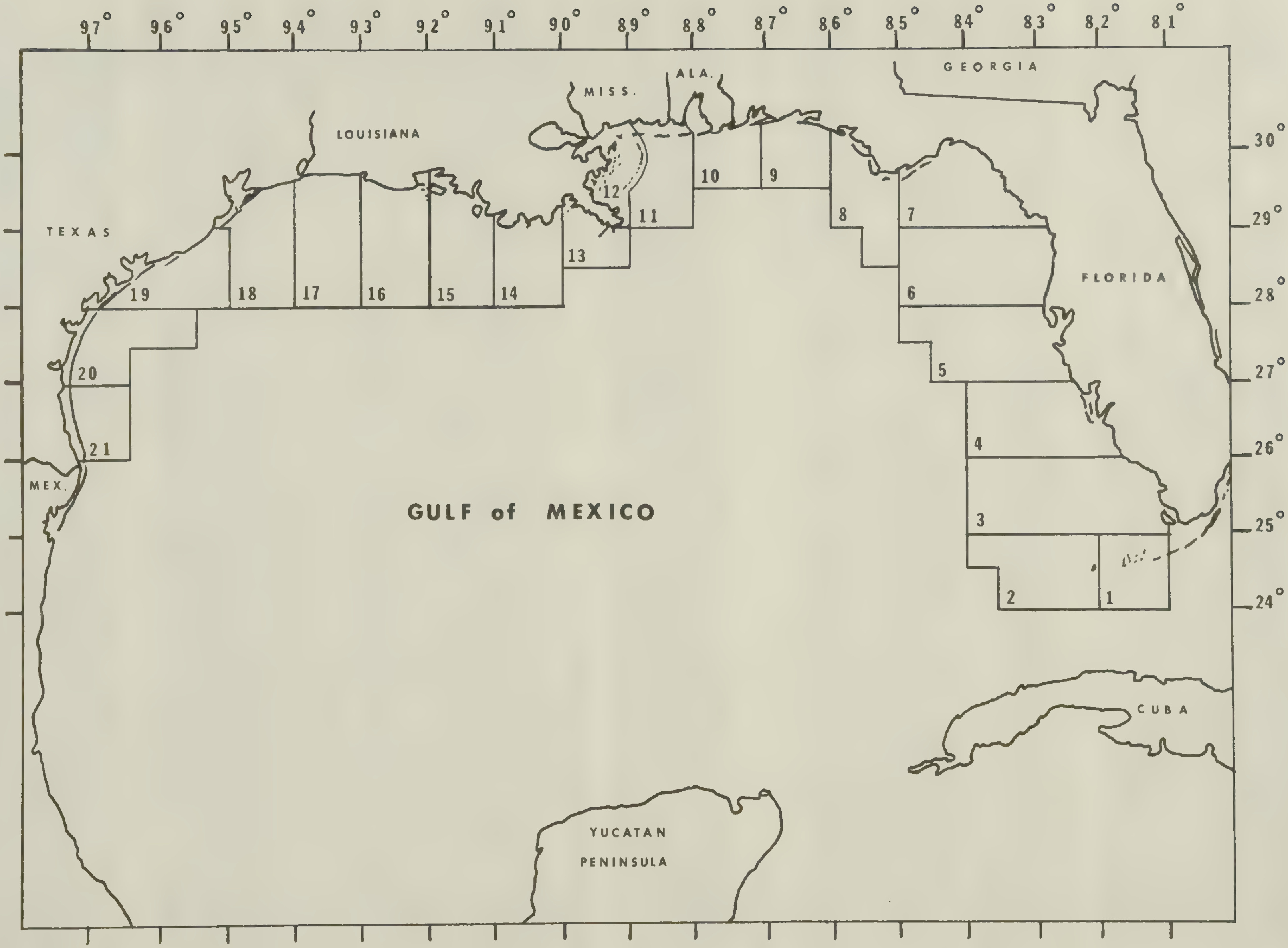
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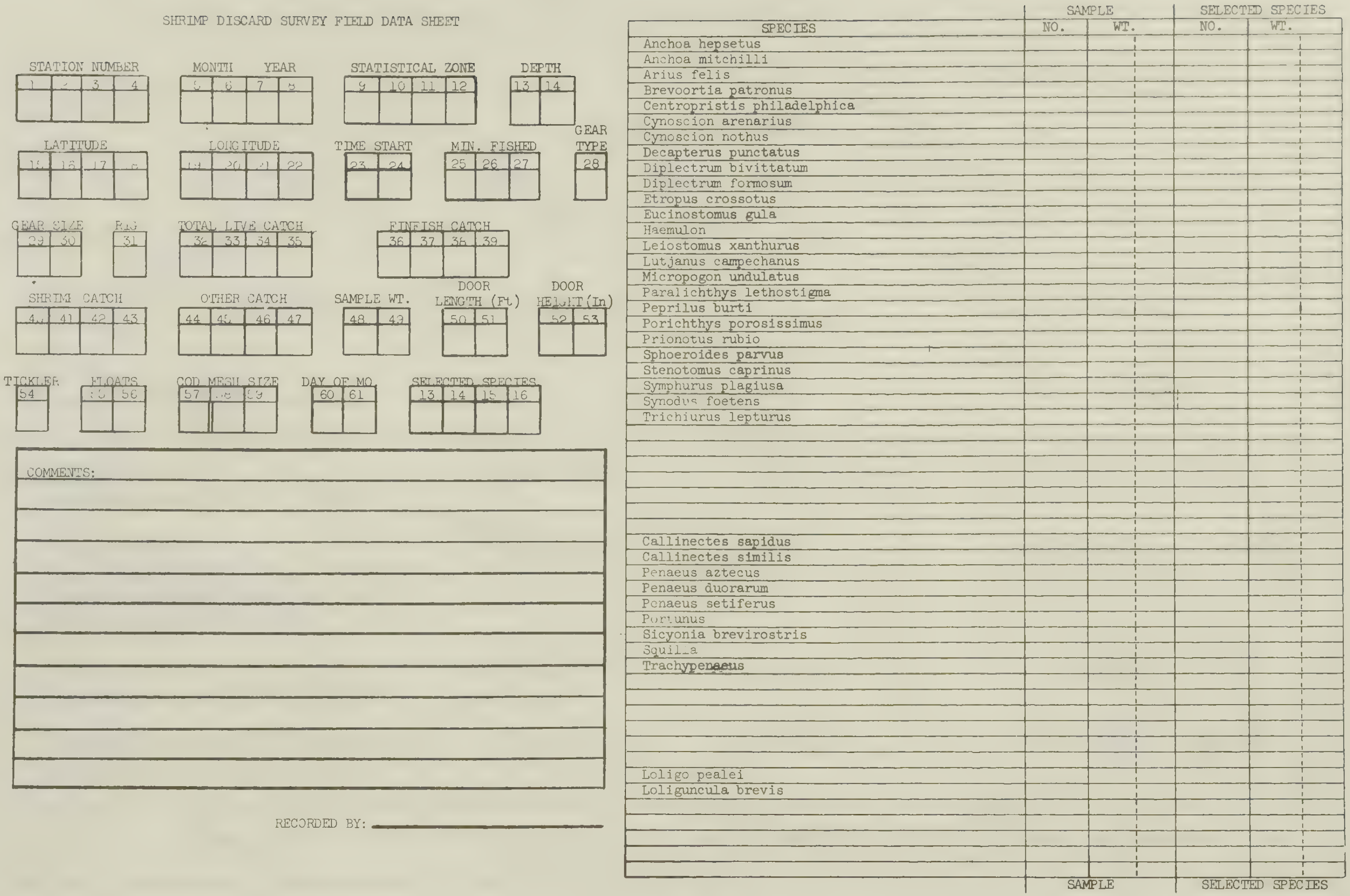
Fig. 3 U.S. Gulf of Mexico shrimp fishing zones

TABLE I

Projected annual finfish bycatch for areas in the U.S. Gulf of Mexico

Locality	FF/S ratio[a]	Shrimp landings (kg)	Projected FF discards (kg)
Northeastern Gulf of Mexico (Shrimp fishing grid zones 1-9)	6.7:1(±1.3:1)	330 916	2 217 138(± 430 191)
Northcentral Gulf of Mexico (Zones 10-16)	18.9:1(±1.4:1)	8 251 702	155 957 160(±11 552 382)
Inland Louisiana Areas (Barataria Bay, Caillou Bay, Lake Barre, Lake Pelto, and Lake Mechant)	3.4:1(±1.0:1)	1 664 824	5 660 401(± 1 664 824)
Northwestern Gulf of Mexico (Zones 17-21)	5.9:1(±1.8:1)	6 143 214	36 244 963(±11 057 785)

[a] FF, finfish; S, shrimp



SHRIMP DISCARD SURVEY FIELD DATA SHEET

STATION NUMBER 1 2 3 4
MONTH 5 6 YEAR 7 8
STATISTICAL ZONE 9 10 11 12
DEPTH 13 14

LATITUDE 15 16 17 18
LONGITUDE 19 20 21 22
TIME START 23 24
MIN. FISHED 25 26 27
GEAR TYPE 28

GEAR SIZE 29 30
RIG 31
TOTAL LIVE CATCH 32 33 34 35
FINFISH CATCH 36 37 38 39

SHRIMP CATCH 40 41 42 43
OTHER CATCH 44 45 46 47
SAMPLE WT. 48 49
DOOR LENGTH (Ft) 50 51
DOOR HEIGHT (In) 52 53

TICKLER 54
FLOATS 55 56
COD MESH SIZE 57 58 59
DAY OF MO. 60 61
SELECTED SPECIES 13 14 15 16

COMMENTS:

RECORDED BY: ____________

SPECIES	SAMPLE NO.	SAMPLE WT.	SELECTED SPECIES NO.	SELECTED SPECIES WT.
Anchoa hepsetus				
Anchoa mitchilli				
Arius felis				
Brevoortia patronus				
Centropristis philadelphica				
Cynoscion arenarius				
Cynoscion nothus				
Decapterus punctatus				
Diplectrum bivittatum				
Diplectrum formosum				
Etropus crossotus				
Eucinostomus gula				
Haemulon				
Leiostomus xanthurus				
Lutjanus campechanus				
Micropogon undulatus				
Paralichthys lethostigma				
Peprilus burti				
Porichthys porosissimus				
Prionotus rubio				
Sphoeroides parvus				
Stenotomus caprinus				
Symphurus plagiusa				
Synodus foetens				
Trichiurus lepturus				
Callinectes sapidus				
Callinectes similis				
Penaeus aztecus				
Penaeus duorarum				
Penaeus setiferus				
Portunus				
Sicyonia brevirostris				
Squilla				
Trachypenaeus				
Loligo pealei				
Loliguncula brevis				
	SAMPLE		SELECTED SPECIES	

Fig. 4 Shrimp discard survey field data sheet

TABLE II

Species composition of finfish bycatch

Locality	Projected FF discard (kg)	Species	Bycatch composition percent	Projected weight (kg)
Northeastern Gulf of Mexico	2 217 138	*Etropus crossotus*	16.5	365 828
		Diplectrum formosum	12.2	270 491
		Eucinostomus sp.	11.8	261 622
		Cynoglossidae	8.1	179 588
		Triglidae	7.8	172 937
		Bothidae	5.6	124 160
		Haemulon sp.	4.6	101 988
		Porichthys porosissimus	4.3	95 337
		Alutera schoepfi	2.4	53 211
		Leiostomus xanthurus	1.5	33 257
		Other species	25.2	558 719
			100.0	2 217 138
Northcentral Gulf of Mexico	155 957 182	*Micropogon undulatus*	45.6	71 116 488
		Stenotomus caprinus	7.7	12 008 701
		Leiostomus xanthurus	7.4	11 540 830
		Cynoscion arenarius	5.2	8 109 772
		Arius felis	4.4	6 862 115
		Cynoscion nothus	3.1	4 834 672
		Prionotus rubio	3.1	4 834 672
		Synodus foetens	2.9	4 522 758
		Trichiurus lepturus	2.7	4 210 843
		Peprilus burti	.8	1 247 657
		Other species	17.1	26 668 674
			100.0	155 957 182
Inland Louisiana Areas	5 660 402	*Brevoortia patronus*	23.7	1 341 515
		Leiostomus xanthurus	19.2	1 086 797
		Micropogon undulatus	17.4	984 910
		Arius felis	10.1	571 701
		Trichiurus lepturus	8.3	469 813
		Cynoscion arenarius	6.0	339 624
		Polydactylus octonemus	2.7	152 831
		Synodus foetens	2.4	135 850
		Paralichthys lethostigma	2.0	113 208
		Menticirrhus americanus	1.4	79 246
		Other species	6.8	384 907
			100.0	5 660 402
Northwestern Gulf of Mexico	36 244 963	*Micropogon undulatus*	38.1	13 809 331
		Cynoscion arenarius	5.2	1 884 738
		Cynoscion nothus	4.6	1 667 268
		Polydactylus octonemus	4.4	1 594 778
		Syacium gunteri	4.0	1 449 799
		Prionotus rubio	3.3	1 196 084
		Stenotomus caprinus	2.8	1 014 859
		Leiostomus xanthurus	2.3	833 634
		Upeneus parvus	2.1	761 144
		Synodus foetens	1.9	688 654
		Other species	31.3	11 344 674
			100.0	36 244 963

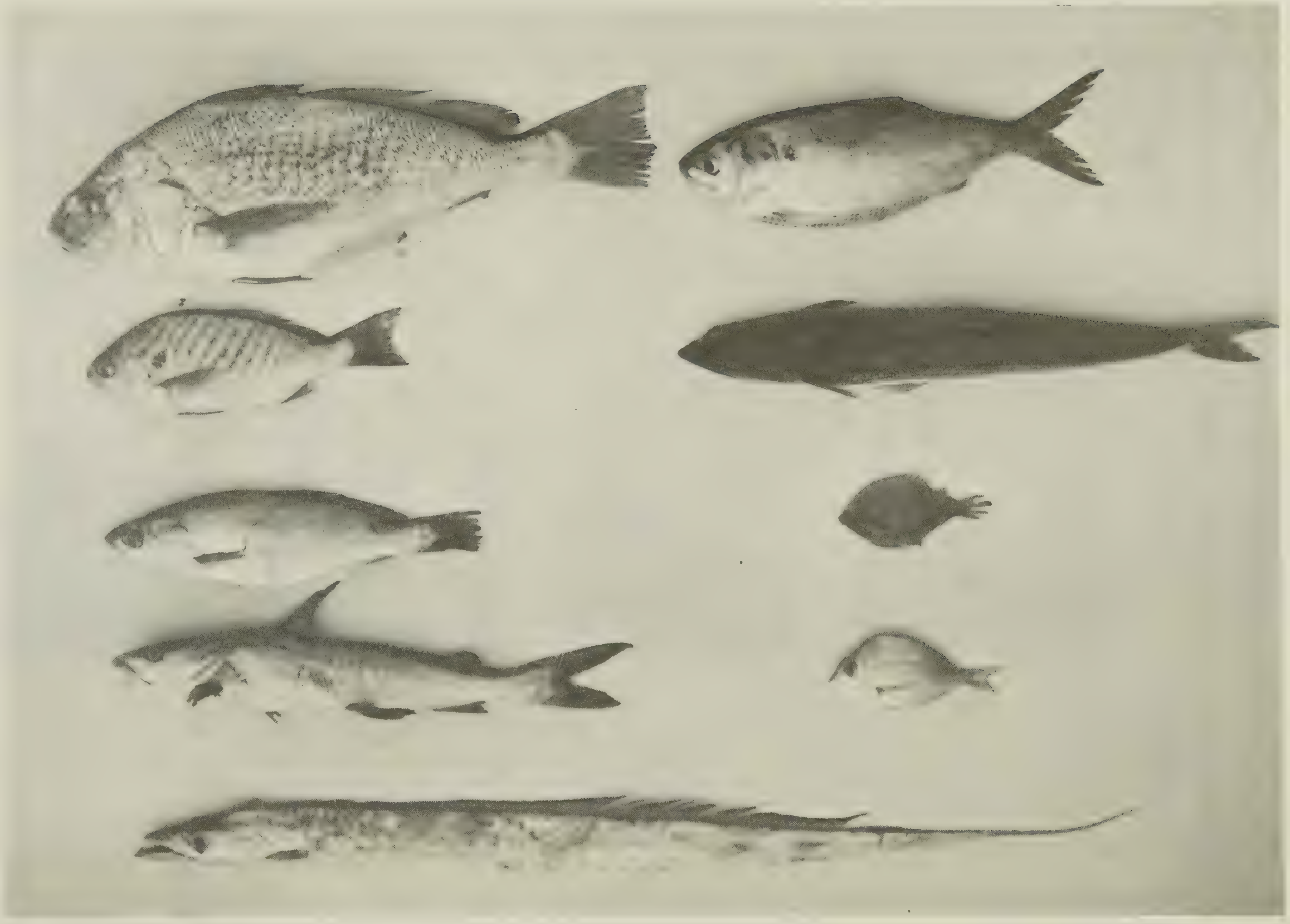


Fig. 5 Major finfish species associated with the Gulf of Mexico shrimp fleet bycatch (Top to bottom, left column first), Croaker (*Micropogon undulatus*), Spot (*Leiostomus xanthurus*), Seatrout (*Cynoscion arenarius*), Sea catfish (*Arius felis*), Silver eel (*Trichiurus lepturus*), Menhaden (*Brevoortia patronus*), Lizardfish (*Synodus foetens*), Fringed flounder (*Etropus crossotus*), Longspine porgy (*Stenotomus caprinus*)

TABLE III

Sizes, weights and possible uses of the northcentral Gulf of Mexico croaker bycatch

Length (cm)	Average weight (g)	Percent	Use	Bycatch weight (kg)	Percent by weight
10	10	2	Bait Petfood Meal	711 160	<1
15	30	68	Minced fish Petfood Meal	20 623 640	29
20	90				
25	190				
30	340	28	Small and Medium Foodfish	43 380 760	61
35	530				
40	800	2	Large Foodfish	6 400 760	10
45	1 150				

6. PRELIMINARY RESULTS

Groundfish survey data were useful in providing baseline bycatch information. These, along with data from the Texas Parks and Wildlife Department and the Louisiana Wild Life and Fisheries Commission, have enabled Project personnel to calculate preliminary estimates of mean fish-to-shrimp catch ratios (Table I). Acquired data were used in connexion with current shrimp fishery statistics gathered by the National Marine Fisheries Service to estimate volumes of discarded finfish (Table I). Data show that the highest discard rates occur in the northcentral Gulf of Mexico, the lowest in the Inland Louisiana area. Although bycatch data are still too few to provide reliable comparisons between offshore (5-50 fath) and inshore (less than 5 fath) zones, preliminary results for certain areas indicate strongly a greater bycatch offshore than inshore. The shrimp grounds off Louisiana fall within this category.

Table II shows the finfish species identified in the bycatch, ranked according to their percentage (by weight) in the catch. In all four Gulf areas mentioned, croaker (Micropogon undulatus) dominate the bycatch both in weight and numbers. This fish, and other dominant finfish species in the U.S. Gulf of Mexico shrimp fishing bycatch, are shown in Fig. 5. A significant part of the bycatch data accumulated thus far comes from the northcentral Gulf. According to the preliminary estimates, this area produces 78 percent of the total U.S. Gulf bycatch. Within this area, croaker is 46 percent by weight of the finfish bycatch.

Croaker are presently being utilized in several products, ranging from bait to foodfish; petfood is the most important economically. Since the Gulf croaker has a diversity of uses and makes up a large part of the bycatch of the northcentral area, Table III is included to show its status. The length/weight frequencies were taken during autumn groundfish cruises; therefore, the bycatch weight percentages in Table III could change when data from other seasons become available.

7. ACKNOWLEDGEMENTS

We are indebted to Mr. C.E. Bryan of the Texas Parks and Wildlife Department, Rockport, Texas, and his staff, who provided the data for the northwestern Gulf area. Also, we thank Mr. Harry Schafer, of the Louisisana Wild Life and Fisheries Commission, and his staff, for the Inland Louisiana information.

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A REVIEW OF RESEARCH BY FLORIDA DEPARTMENT OF NATURAL RESOURCES ON SPECIES OF TRANS-CARIBBEAN IMPORTANCE

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CONTENTS

1. INTRODUCTION
2. LOBSTER
3. TURTLES
4. SAILFISH
5. CONCLUSIONS

Abstract

A comprehensive survey is made of the history, output and plans for Department research in the northern Caribbean and southern Gulf of Mexico. Emphasis is placed on studies of spiny lobsters (Panulirus argus), sea turtles and billfishes as resources between Florida and other Caribbean locales. Spiny lobster investigations are discussed in respect to recruitment of postlarvae and young juveniles, especially with regard to techniques for establishing rates and locations of postlarval settling. The results of many years of rearing and tag-release studies on laboratory husbandry and migrations of green turtles are presented. A report is made of the Laboratory's long-standing project on population dynamics of the Atlantic sailfish, with suggestions of how such work might be conducted elsewhere and the extent to which the Caribbean may contribute to population stabilities throughout the western Atlantic. The summary contains recommendations about research planning needs and opportunities for cooperative programmes to more thoroughly understand and manage these important animals.

Resumen

El trabajo presente un panorama completo de la historia y resultados de las investigaciones hechas por el Departamento en el norte del Caribe y el sur del Golfo de México, y los planes para el futuro. Se presta atención sobre todo a los estudios sobre la langosta (Panulirus argus), las tortugas marinas y los peces aguja, recursos que se encuentran en Florida y otras zonas del Caribe. Se presentan los resultados de las investigaciones sobre reclutamiento de formas poslarvales y juveniles de langosta, atendiendo sobre todo a las técnicas utilizadas para determinar los índices de distribución de las formas poslarvales y las zonas donde se asientan. Se presentan también los resultados de varios años de trabajos de cría en laboratorio y de algunos experimentos de marcado y suelta para determinar los movimientos migratorios de las tortugas verdes. Se informa sobre el proyecto realizado por el Laboratorio para estudiar la dinámica de las poblaciones del pez vela del Atlántico, sugiriendo cómo pueden realizarse trabajos análogos en otras zonas y en qué medida el Caribe puede contribuir a la establilidad de las poblaciones del oeste del Atlántico. En resumen se hacen recomendaciones sobre la necesidad de planificar las investigaciones y sobre las posibilidades de iniciar programas de cooperación para conocer mejor tan importantes recursos y regular su explotación.

1. INTRODUCTION

Our purpose is to present a résumé of how, and for how long, we have researched the biology of three major groups of marine animals of pan-American importance in the southwestern Atlantic, Caribbean and southern Gulf of Mexico. We hope to share this knowledge reciprocally so that all peoples benefit from the results of scientific cooperation in marine research around the Caribbean.

2. LOBSTER

One of the best trans-Caribbean resource species is the indigenous spiny lobster, or langosta, Panulirus argus. Approximately 30 000 metric tons are landed each year from this fishery, which extends from the southeastern coast of the United States, throughout the Caribbean to Brazil.

We began on the life and distribution of lobster larvae in Florida waters in 1944, when we were called the Florida Board of Conservation. These investigations, and others after 1950, showed Florida waters to provide substantial numbers of planktonic larvae but, because of their long period of six-months' larval development, they probably drifted elsewhere to settle as postlarvae. As a consequence of this discovery, coupled with our knowledge of the major currents of the Caribbean and southern Gulf of Mexico, we feel certain at least a substantial part of the lobster fishery in our Keys is recruited from larvae originating in breeding populations to the south and southwest of us. We became interested, therefore, in the locations, rates and seasons of postlarval settling so that we could make meaningful management recommendations. In 1964 we designed a simple and effective sampler for postlarvae, the Witham habitat, and are presently using it to obtain more details of its efficiency and monitor lobster recruitment in our southern Keys. The results of these studies, together with many others regarding behaviour, migrations, growth rates and other facets of lobster biology and fishing technology, represent our contributions toward a better understanding of this large and very valuable Caribbean resource.

3. TURTLES

Our Department, with many others, has long been active throughout the Caribbean in sea turtle (tortuga) investigations; these have shown turtles to be long-distance travellers here, just as in other parts of the world. Green turtles, Chelonia mydas (Linné), are hatched, grown, tagged and released at several locations in Florida each year by our Laboratory on the southeast coast. Through the kindness of those who recover them, tag returns show that these animals appear as far south as Venezuela and Surinam.

Turtles nest on sheltered beaches along both coasts of Florida during spring and summer; notably C. mydas, the loggerhead Caretta caretta (Linné) and Dermochelys coriacea (Linné). Coastal development, here and elsewhere, is gradually reducing the number of acceptable beach sites which, in turn, has seriously threatened population size and stability, particularly of C. mydas. For this reason, we hope to expand our surveys of turtle nesting beaches in order to establish the characteristics that make a beach "popular" as a turtle rookery and then to use this information in recommending where beach preserves should be established so that natural populations will be preserved.

We also plan to expand our hatching and rearing operations and add continuous breeding capabilities to our new facilities, thus making a larger contribution to the first-year-class portion of turtle populations in our waters. Great improvements should be possible with this technique since theoretical models have shown that it is possible to support wild populations in this way and since yearlings are less susceptible to disease and predation than hatchlings.

4. SAILFISH

The Atlantic sailfish (Istiophorus platypterus) is one of the Caribbean's most respected and outstanding sport resources. Anglers from all over the world come to our shores to catch this spectacular gamefish. Florida's southeastern coast is host each year to a number of tournaments in which sailfish is considered a prize catch. Contestants in these tournaments have cooperated with fishery biologists for many years by releasing their catches after they have been tagged so their migrations and rates of growth can be recorded. We have recently used elecontronic sound-producing tags on sailfish to track them with sonar. For the first time it was demonstrated that these fish survive the catch and tag process and appear to move normally thereafter.

Our fishable sailfish population seems to be maintaining itself in spite of an ever-increasing number of anglers and fish taken. We realize, however, that it is necessary to follow tournament catches and others each season both in order to add continually to our knowledge of the biology of these fish and to be in a position to put forward recommendations concerning management practices for the fishery, should they ever be required. We are also searching continually for information regarding sailfish spawning and nursery areas, one of which we suspect to be in the north central Caribbean. A new project at our Laboratory is a study of the food of sooty terns nesting in Dry Tortugas. Since these birds often feed on pelagic fish larvae and post-larvae, by this method we hope to obtain more data regarding the location of spawning sites of both sailfish and other important fish species.

5. CONCLUSIONS

Although our research concerning some of these species has been going on for more than twenty years, there is still much knowledge to be discovered if we are to put forward recommendations to help sustain and manage them across the Caribbean. We know that many others have the same responsibilities and interest and we hope to be joined in cooperative efforts to get this knowledge. At our present stage of research it would seem advisable to pool all the research data available in the different CICAR countries concerning these species before deciding our next step in the research programme.

We suggested the first step in this process to be the discussions concerning cooperative turtle research programmes at our Florida and Interregional Turtle Conference held at Jensen Beach, Florida, on 24 and 25 July 1976. Over 130 scientists we know to be interested in turtles throughout the world were invited. At the CICAR II Symposium an open invitation was given to all participants in order to cover any possible oversight.

It might be possible to plan or initiate similar discussions here with regard to spiny lobsters, sailfish and other species in which there is a common interest, if a future schedule will permit us to get together. We would welcome suggestions on this matter.

We will close by expressing the hope that we have helped provide an understanding, however general, as to what our work has accomplished with regard to some major species in which all the CICAR countries have interest. It is also our hope that we will hear soon from many who would like to join us in any cooperative research. Toward that end might I also extend an invitation to the librarians of the home institutions of the participants to write to ours, requesting a list of the free publications available on Florida's marine resources, with the hope some of our information may be of benefit.

AN OVERVIEW OF THE FISHERY RESOURCES OF THE WEST CENTRAL ATLANTIC REGION

by

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CONTENTS

1. INTRODUCTION
2. STATUS OF THE FISHERY
3. MATERIAL AND METHODS
4. GROUNDFISH
5. COASTAL PELAGICS
6. SNAPPER-GROUPER
7. CONCLUSIONS
8. REFERENCES

Abstract

The total annual harvest in the Western Central Atlantic is about 2.8 million t with a reported commercial production of 1.4 million t and estimated recreational catch of 0.4 million t and about 1 million t of fish caught and discarded at sea by the various shrimp fisheries.

The estimated potential yield for the entire area for all species except high-sea pelagic fishes is of the order of 5.3-6.9 million t.

The total potential for groundfish is put at 2.5 million t, of which more than 50 percent is available in the Gulf of Mexico. A large portion of this resource is presently being caught incidentally by shrimp boats and discarded at sea. Considerable potential exists on the Campeche Bank for porgies and grunts and for sea trouts along the shelf off the northeast coast of South America. Estimates of the groundfish resources were obtained from extensive trawling surveys and are considered reliable.

The estimate of snapper-grouper potential is 519 000 t and is based on a simple, directly determined density off Jamaica and applied to catch ratios throughout the Caribbean Sea. Although the procedure is not very accurate, it is good enough to show that catches could be greatly increased.

With the exception of the menhaden along the U.S. coast, for most of the species of coastal pelagic fish, only a very rough indication of the order of magnitude of the resource can be provided. The potential yield may range from 1.3 to 2.9 million t.

Although increased production can be realized from snapper-grouper, groundfish and coastal pelagic stocks, some of these resources are much more scattered than resources in other regions, are spread over large areas and the density per unit area is not usually very high. Factors which will influence development of new fisheries will include distribution, availability of stocks, economical techniques for harvesting, as well as development of suitable markets.

Resumen

La producción anual total del Atlántico centro-occidental es del orden de 2,8 millones t así desglosadas: 1,4 millones t de producción comercial, capturas deportivas del orden de 0,4 millones t, y 1,0 millones t de peces capturados y descartados en alta mar en las pesquerías de camarón.

El rendimiento potencial estimado de todas las especies de la zona, exceptuados los peces pelágicos de alta mar, es del orden de 5,3-6,9 millones t. El rendimiento potencial de peces de fondo se calcula en 2,5 millones de toneladas métricas, de las cuales más del 50 por ciento se encuentran en el Golfo de México. Las embarcaciones camaroneras capturan actualmente una proporción importante de esos recursos, que descartan en alta mar. El banco de Campeche ofrece grandes posibilidades para la captura de pargos y roncadores y a lo largo de la plataforma continental de la costa nordeste de América del Sur abundan las truchas de mar. Las estimaciones sobre el rendimiento de los peces de fondo son resultado de vastos reconocimientos al arrastre y se consideran fidedignas.

Las estimaciones del rendimiento potencial de meros y pargos arrojan una cifra de 519 000 t, y se basan en la determinación directa de las poblaciones existentes frente a Jamaica, extendida luego a todo el Caribe sobre la base de los índices de captura. Aunque el procedimiento no es muy exacto, basta para mostrar que podrían aumentarse notablemente las capturas.

Por lo que se refiere a la mayoría de las especies pelágicas costeras, con excepción del menhaden que se encuentra a lo largo de la costa de los Estados Unidos, no es posible ofrecer más que una indicación muy aproximado del orden de magnitud de los recursos. El rendimiento potencial podría ser del orden de 1,3 a 2,9 milliones t.

Aunque sería posible aumentar la producción de pargos y meros, peces de fondo y peces pelágicos costeros, algunos de estos recursos están mucho más dispersos que los de otras regiones, se extienden por zonas muy amplias y la densidad por unidad de superficie no es de ordinario muy elevada. Entre los factores que influirán en la creación de nuevas pesquerías figuran la distribución, la disponibilidad de poblaciones, la preparación de técnicas económicas de explotación y la creación de mercados adecuados.

1. INTRODUCTION

The Western Central Atlantic region is one of the underexploited ocean areas of the world, though it supports some important fisheries. In 1974 the total commercial harvest amounted to about 1.4 million t.

Gulland (1971) estimated the total potential yield for the demersal stocks of the entire region to be 1.5 to 2.5 million t with 2.5 to 3.5 million t for the pelagic stocks. Klima (1975) updated the estimates of Gulland and concluded that the total potential for the entire region was 4.8 to 6.3 million t. This paper summarizes and updates Klima's (1975) status of stocks report.

2. STATUS OF THE FISHERY

Since 1970, total annual production in the Western Central Atlantic has been over 1.4 million t (Table I). The U.S.A. and Mexico are the largest producers. The largest part of the total ocean harvest of this region is obtained from marine fish species. The herring-like fish contribute 600 000 t of catch a year and following, in order of importance, are the sea basses, shrimps and oysters. The U.S.A., which has landed over 800 000 t annually during the past few years, produced 904 000 t of fish valued at U.S.$ 332 million in 1975 (Table II). Most of the landings consisted of menhaden and shrimp.

Besides the commercial fishery, there is a substantial recreational fishery in the U.S.A.; Deuel (1973) has estimated the catch from this to be 404 000 t (Table III). The catch composition of the major recreational fish species for the southeastern U.S. coast, the eastern and the western Gulf of Mexico is given in Table IV.

3. MATERIAL AND METHODS

The data and methods of estimating standing stock and potential yield have been described by Klima (1975); all estimates of fish density from trawl surveys were adjusted for the percent escapement from the specific trawl.

3.1 The Basic Data Sources

(1) Twenty years of exploratory fishing data - National Marine Fisheries Service (NMFS)

(2) MARMAP Groundfish Survey

  (a) South Carolina Wildlife and Marine Resource Department
  (b) Pascagoula Laboratory - NMFS

(3) Trawl survey data

  (a) Middle Atlantic Coastal Fisheries Center
  (b) Gulf Coastal Fisheries Center
  (c) Southeast Fisheries Center
  (d) UNDP/FAO Fishery Development Project
  (e) La Salle Survey
  (f) Coquette Survey

(4) Published material

TABLE I

Catch by major species groups
(in '000 t)

	1970	1971	1972	1973
Total catch	1 440	1 639	1 463	1 405
Crustaceans				
Crabs (blue/stone)	31.5	31.3	29.1	35.5
Lobster	17.0	17.6	17.9	19.3
Shrimps (all)	163.5	171.5	173.2	149.1
Other crustaceans	4.1	4.5	3.9	3.8
Molluscs				
Snails (Conchs)	1.0	1.2	1.6	3.0
Oysters	177.0	179.4	135.6	139.0
Mussels	0.2	0.1	0.4	0.4
Scallops	10.9	11.6	7.6	10.8
Clams	11.4	6.1	8.0	11.7
Squid	2.1	3.5	5.6	4.3
Other	4.2	4.3	4.9	2.6
Turtle	1.5	1.6	2.0	1.6
Marine fishes				
Flounders	2.5	2.2	-	3.3
Cods	-	-	-	-
Redfish	145.5	144.1	207.0	175.1
Jacks, mullets	43.6	46.6	49.6	50.7
Herrings	647.3	858.2	635.0	602.9
Tunas	40.4	44.8	37.3	57.2
Mackerels	1.2	2.3	1.9	1.4
Sharks	7.2	7.7	7.9	10.0
Other	92.2	92.7	121.8	125.9

Source: FAO 1973 Yearbook

TABLE II

U.S. commercial landings
('000 t and U.S.$ 1 million)

Area	1971		1972		1973		1974		1975	
	Weight	Value	Weight	Value	Weight	Value	Weight	Value	Weight	Value
South Atlantic	116	41.3	129	44.3	109	56.7	136	47.7	149	60.6
Gulf of Mexico	951	199.9	719	223.4	702	268.1	804	240.8	755	271.1
Total	1 067	241.2	848	267.7	811	324.8	940	288.5	904	331.7

TABLE III

U.S. marine recreational catch by region in 1970
('000 t)

Area	Weight	Number of fish	Number of anglers
South Atlantic	183	184.2	1.81
East Gulf of Mexico	152	188.9	1.48
West Gulf of Mexico	67	97.7	0.87
Total	404	470.8	3.53

TABLE IV

U.S. catch of major recreational species in 1970 in the southeastern coast and in the Gulf of Mexico

Fish species	Southeastern coast	East Gulf of Mexico	West Gulf of Mexico
	t	t	t
King mackerel	15 849	11 104	1 351
Jacks	15 036	1 528	555
Dolphins	12 613	968	-
Grunts	11 776	3 227	1 958
Sea trout (spotted)	11 358	18 538	18 365
Groupers	10 941	7 228	418
Porgies	10 913	9 671	2 574
Snapper (yellowtail)	9 146	369	-
Bluefish	8 741	159	593
Snook	8 145	15 189	-
Catfish	7 516	8 074	14 510
Drum red	6 059	11 576	12 485
Drum black	5 499	5 899	7 301
Croakers	2 678	6 687	21 796
Sharks	228	529	6 270
Sea trout (sand)	10	4 239	9 582

4. GROUNDFISH

4.1 Gulf of Mexico and Southeastern U.S. Coast

Groundfish constitute perhaps the second largest resource, by volume, in the southeastern U.S.A., after menhaden. There are about 175 species, of which the sciaenids (croaker, spot, drums and sea trouts) are the most important. They form a large proportion of the catch of the commercial and sport fisheries in the Gulf of Mexico, constituting about 98 percent of the industrial groundfish and foodfish and most of the finfish discard of the shrimp fleet. Groundfish are mostly used in production of fish meal and pet food. The most productive area for groundfish is the north central Gulf of Mexico from Pensacola, Florida to Galveston, Texas and, particularly, the Mississippi River Delta (Gutherz et al., 1974). Further, a large volume of groundfish is discarded from shrimp trawls.

4.1.1 Shrimp fleet discard

Shrimp fishing entails not only the harvesting of shrimp but the incidental, and often unwanted, capture of fish, molluscs and other crustaceans and marine animals. The quantity of groundfish discarded has only recently been estimated from preliminary information collected by the Southeast Fisheries Center at Pascagoula in cooperation with Louisiana Wildlife and Fisheries, Texas A & M University and Texas Parks and Wildlife (Table V).

The ratio of fish discards to shrimp caught was obtained from observation on commercial shrimp vessels and research vessels working with a commercial fleet and from MARMAP groundfish cruises conducted in shrimp areas.

Estimates of total fish discards are obtained by multiplying the commercial shrimp catch by the observed discard ratio of fish to shrimp in the Gulf of Mexico for the period 1972-1974. The discard ratio varied not only with the fishing grounds but with inshore and offshore habitats. The discard ratio for inshore areas was significantly less than that for offshore areas.

The quantity of fish discarded by the shrimp fleet is estimated to range from about 690 000 to over 900 000 t annually (Klima, 1975). The central northern Gulf area accounts for almost half of the fish discards, while the U.S. coastal area from Florida to the Mexican border accounts for about 70 percent of the discards in the entire Gulf of Mexico.

4.1.2 The fishery

In 1952 a groundfish fishery in the northern Gulf of Mexico was established. The catches increased steadily and, in 1958, reached 34 000 t. Between 1958 and 1966 the annual catch fluctuated around this level but, in 1967, production rose to 45 000 t (Table VI). The available data show that in 1974, Mississippi and Louisiana had a total catch of 53 000 t, worth U.S.$ 2.8 million. On the average, croaker, spot and sea trout make up 70 percent by weight of the total annual industrial catch.

The U.S. catch of croakers and spot for human consumption was 12 300 t in 1973 (Table VII). In 1970, the estimated groundfish catch by saltwater anglers was 197 000 t in the Gulf and 136 000 t in the southeastern states. But the total catch for the Gulf of Mexico and southeastern states is about 279 000 and 145 000 t, respectively. Considering the fish discards, the catch approached 914 000 and 357 000 t in the Gulf of Mexioo and southeastern states, respectively.

On the Campeche Bank, Cuba and the U.S.S.R. harvest porgies (Sparidae) and grunts (Pomadasyidae). Commercial production probably began about 1966 and since then it has varied tremendously, the annual catches having ranged from 8 000 to over 70 000 t. While the trawl catches consist mostly of porgies and grunts, snapper make up about 24 percent and grouper 11 percent of the species harvested.

TABLE V

Gulf of Mexico discard ratio shrimp catch (heads-off) and estimated discard of groundfish correction to heads-on (1.6) in t

Statistical area	Shrimp catch (heads-off)					Groundfish correction to heads-on (1.6)		
	Discard ratio	Confidence limits C.L.90	1972	1973	1974	1972	1973	1974
11	17.13	± 3.81	3 724	1 719	2 182	102 040 ± 22 716	47 101 ± 10 451	59 802 ± 13 281
12	7.08	± 2.44	168	145	86	1 887 ± 653	1 669 ± 581	943 ± 363
13	20.17	± 1.87	3 320	2 794	2 545	107 121 ± 9 943	90 138 ± 8 346	82 156 ± 7 620
14	20.02	± 2.96	1 896	1 025	866	60 745 ± 8 999	32 803 ± 4 862	27 724 ± 4 136
15	15.72	± 3.31	4 849	3 198	3 611	121 998 ± 25 692	80 413 ± 16 909	90 791 ± 19 087
16	10,76	± 3.11	2 839	2 141	1 733	48 915 ± 14 152	36 868 ± 10 669	29 828 ± 8 636
11–16 (inshore)	3.12	± 0.92	11 553	8 065	8 677	57 697 ± 16 983	40 279 ± 11 902	43 327 ± 12 773
1–10	8.27	± 0.75	5 534	6 854	7 253	73 228 ± 6 677	90 719 ± 8 201	95 944 ± 8 709
17–21	7.00	± 3.00	22 534	16 955	18 774	252 415 ± 108 137	189 928 ± 81 356	210 249 ± 90 138
22–30	8.27	± 0.75	3 896	2 581	2 985	51 528 ± 4 645	34 183 ± 3 121	39 481 ± 3 556
31–40	8.27	± 0.75	1 565	2 014	1 042	20 684 ± 1 887	26 635 ± 2 394	21 700 ± 1 960
17–21 (inshore)	3.12	± 0.92	3 261	3 946	2 608	16 257 ± 4 790	19 668 ± 5 806	12 991 ± 3 847
11–16						500 404 ± 99 137	329 272 ± 63 721	334 570 ± 65 899
Rest of Gulf						414 112 ± 126 135	361 132 ± 100 879	380 365 ± 108 209
MARMAP – Survey area (11–15)						451 489 ± 84 985	292 404 ± 53 052	304 742 ± 57 263
Total Gulf						914 516 ± 225 272	690 405 ± 164 600	714 935 ± 174 107

One reason for the great variation in the catches is that the availability of porgies and grunts depends on the bottom temperature on the Campeche Bank (Olaechea, 1975). In the autumn of 1972 the bottom temperature on the eastern portion of the Bank was above 26°C and the density of porgies and grunts was much lower than in the spring, summer or winter of 1972 (Olaechea and Sauskan, 1974). Gonzáles (1973) found a good relationship between catch rates and water temperature at a depth of 100 m on the eastern edge of the Bank. Apparently the fish move down the slope into cooler water when the bottom water on the Bank itself is too warm.

TABLE VI

Trends in the Gulf of Mexico industrial groundfish fishery
based on 5-year averages (1959-73)

Year	'000 t	% increase	U.S.$ (million)
1959-63	41.3	-	1.4
1964-68	45.2	10	1.6
1969-73	46.7	3	2.0

TABLE VII

Tablefood fish catch (t)

Year	Croaker		Spot		Croaker and spot
	South Atlantic	Gulf	South Atlantic	Gulf	Total
1970	408	3 357	1 497	136	5 398
1971	454	4 627	2 449	227	7 757
1972	1 905	5 262	2 676	181	10 024
1973	1 996	7 484	2 812	91	12 383

4.1.3 Status of stocks

The potential yield of groundfish has been estimated by Bullis and Carpenter (1968) to be 3 million t in the Gulf of Mexico. Gulland (1971) estimated the potential yield to be 750 000 t. Klima (1975) estimated the standing stock of inshore groundfishes in the Gulf of Mexico to be 3.9 million t.

The potential yield for inshore groundfish in the Gulf of Mexico is 1 509 000 t. The figure was estimated by using the potential yield equation given by Gulland (1971), with a slight modification by Cadima: $Y\ max = 0.5 \times (Z_2 \times \bar{B}_2)$, where Z_2 is the total mortality and B_2 is the standing stock of the exploited populations. The total catch is 914 000 t and the potential surplus production is 595 000 t; however, 636 000 t of groundfish is presently discarded annually. Hence, the potential increase for the area is about 1 231 000 t.

Significant increases in production could be realized in the northern Gulf of Mexico and on the Campeche Bank. Currently, in the north Gulf, almost 640 000 t of groundfish are produced annually, of which more than 500 000 t are discarded. Production could be increased by about 230 000 t but, with utilization of the discards, the area could increase production by more than 700 000 t annually. The Campeche Bank area has a potential for increasing production from around 20 000 to over 300 000 t, consisting mostly of porgies and grunts.

The offshore potential in the Gulf of Mexico is minimal, with a potential of perhaps 9 000 tons. Offshore hake Merluccius albidus show promise for commercial exploitation with a 14 000 t estimate of standing stock (Rohr and Gutherz, MS.)

4.2 The Southeastern U.S. Coast - Cape Hatteras to Cape Kennedy

The southeastern continental shelf region of the U.S. coast consists of five general habitat types: coastal, open-shelf, live-bottom, shelf-edge and lower-shelf, and each habitat harbours a distinctive association of demersal fish species (Struhsaker, 1969). The coastal habitat has a sandy-mud bottom and extends to a depth of 15-18 m. It is in this habitat that drums and croakers occur abundantly. The open-shelf habitat extends from an 18-55 m depth. This area has little potential for foodfish. However, there are occasional catches of scup and filefish, suggesting that the area might be able to support a small industrial fishery.

The live-bottom habitats are small areas, rich in sessile invertebrate fauna and lying within the open-shelf habitat. These areas have the highest potential for tablefish. During exploratory trawling, large catches of snappers, groupers, porgies and other species were made with a New England-type otter trawl. The shelf-edge habitat has a mixture of smooth, and highly broken, bottom and runs parallel to the edge of the continental shelf at depths of 54-110 m. This area has a large concentration of snappers, groupers and porgies. Trawling is often impractical in the rougher areas of this habitat, but the fishery resource could be harvested by handlines and traps. The lower-shelf habitat, with a smooth-mud bottom, extends from 110 to 183 m and has large concentrations of butterfish and spotted hake.

4.2.1 Catch trends

Over 9 000 t of assorted groundfish were landed off the southeastern U.S. coast in 1971. The total sport catch along that coast was 183 000 t, of which 47 000 t consisted of tunas, billfishes, mackerel, dolphin and barracudas (Deuel, 1973). Hence, a total catch of about 136 000 t is produced annually.

The discard ratio of fish to shrimp for the areas is 3.8. It is estimated that 262 000, 212 000 and 206 000 t of fish were discarded by shrimp vessels in 1972, 1973 and 1974 respectively. If at least 200 000 t of fish are discarded annually, the catch of finfish along the U.S. coast from Cape Hatteras to Key West is about 357 000 t.

The standing stock is estimated to be 1.5 million t by Bullis and Carpenter (1968) and Gulland estimated the potential yield to be 380 000 t.

Klima (1975) estimated the average standing stock for the inshore areas to be 1 948 000 t. The total inshore production is 357 000 t. Fishing mortality is estimated at 0.2 and, assuming a natural mortality of 0.5, the total mortality is $Z = 0.7$. The potential yield therefore would be about 681 000 t (Table VIII). At least 12 percent of the biomass is associated with the live-bottom area, which is perhaps only 2 percent of the total area from Cape Hatteras to Cape Kennedy. The live-bottom reef areas provide the greatest potential for easily increasing production, with a potential of, perhaps, around 70 000 t.

The offshore stock is almost unexploited and the standing stock is estimated to be 101 000 t. The potential yield for this areas is about 25 000 t; however, it is widely dispersed.

4.3 Northeast Coast of South America

Recent trawl surveys conducted between French Guiana and Colombia show a wide disparity in the density of groundfish. In general, waters shallower than 37 m were more productive than offshore areas (i.e., 37-183 m). The most productive area is off Surinam, with a density around 160 kg/ha, and Guyana, with a density of 55 to 95 kg/ha. In depths between 37 and 183 m, the density ranged from 57 to 83 kg/ha for Guyana to French Guiana (Klima, 1975).

TABLE VIII

Estimates of harvest, best standing stock and yield for groundfish
(in '000 t)

	North Gulf of Mexico		Florida West Coast		Campeche Bank	U.S. Atlantic Coast North Carolina–Florida	
	0–110 m	110–548 m	0–110 m	110–548 m		0–110 m	110–548 m
Area (km^2)	111 210	44 070	179 280	72 120	89 202	125 010	50 480
Harvest							
Commercial 1973	54	–	–	–	27[a]	9[b]	–
Recreational 1970	66	–	131	–	–	136	–
Discards 1973	519	–	91	–	26	212	–
TOTAL	639	–	222	–	53	357	–
Standing stock	1 387–1 928	66–126	611–895	101–141	608–1 533	1 431– 2 710	79 135
Best estimate	1 928	96	753	121	1 171	1 948	101
F	.40	–	.35	–	.05	.20	0
Yield	867	24	320	30	322	681	25
Catch kg/ha							
Present	58	–	12	–	6	29	–
Potential	78	5	18	4	36	55	5

[a] 1974
[b] 1971

The standing stock for the entire area is estimated to be 1 121 000 t, an average density of 56 kg/ha (Table IX). The potential yield, using Gulland's (1971) equation, is 280 000 t, assuming a natural mortality of 0.5. Gulland (1971) estimated a standing stock of about 350 000 t, with a potential yield of 160 000 t, assuming a 50 percent escapement from the trawl and a natural mortality of 0.6.

5. COASTAL PELAGICS

5.1 Menhaden

Menhaden is the largest fishery in the Western Central Atlantic area. Two species are of commercial importance, the Atlantic menhaden (*Brevoortia tyrannus*) and the Gulf menhaden (*B. patronus*). The fishery is conducted along the U.S. Atlantic coast from Florida to Maine, but centred around the mid-Atlantic region, and in the northern Gulf of Mexico from Florida to Texas. Catches in the Atlantic have fluctuated widely in recent years from a peak of 659 000 t in 1959 to a low of 161 000 t in 1969, with current production in 1975 at 250 000 t.

The Gulf fishery expanded in the period following the second world war. Catches increased to a peak of 728 000 t in 1971, and have declined to around 500 000 t over the last four years.

5.1.1 Status of stocks

5.1.1.1 Gulf fishery

Landings of Gulf menhaden in 1975 amounted to 542 000 t, or 6 percent less than in the 1974 season. To achieve this production fishing effort increased by 11 percent over 1974. Age-1 menhaden comprised about 50 percent of the catch in 1975 and 1974, and 41 percent were age-2 fish.

Chapoton (1972) analysed the trends in catch and effort of the menhaden fishery, using Schaefer's (1954) model. He estimated an MSY of 480 000 t, corresponding to a fishing effort of 460 000 vessel-ton weeks (Fig. 1). By updating the model with recent catch and effort data, Chapoton estimated the MSY to be about 500 000 t and 482 000 vessel-ton weeks. He indicated that fishing effort will increase by 6 percent in 1976, resulting in a catch of about 603 000 t. If maximum landings have been achieved, then catches after 1976 could decrease with current levels of fishing.

5.1.1.2 Atlantic fishery

Landings of Atlantic menhaden in 1975 amounted to 250 000 t with an increase of 6 percent in fishing effort over 1974. Since 1971, fishing effort has increased 36 percent, yet the catch is about the same.

The National Marine Fisheries Service has concluded that juvenile abundance of menhaden in 1975 is less than in 1974 and less than it was 4 or 5 years ago.

Schaaf (1975) updated the Schaefer yield model and has estimated an MSY of 560 000 t with 630 vessel-weeks of effort (Fig. 2). The author clearly points out two distinct areas of the fishery.

The first period in the fishery occurred from 1955 through 1962, when the total numbers of menhaden caught out of a year class averaged 3 000 million fish (standard error equals 0.8 thousand million), and the weight landed annually during this period averaged 596 000 t (standard error equals 25 000). The second period occurred from 1963 through 1973, when catches averaged 266 000 (standard error equals 20 000) t from virtual populations that averaged only 1.3 thousand million (standard error equals 0.1 thousand million). From 1968 through 1971 there has been a 30 percent reduction in effort which, the NMFS feels, is partly responsible for allowing the catches to rebound in 1972. That year, landings were

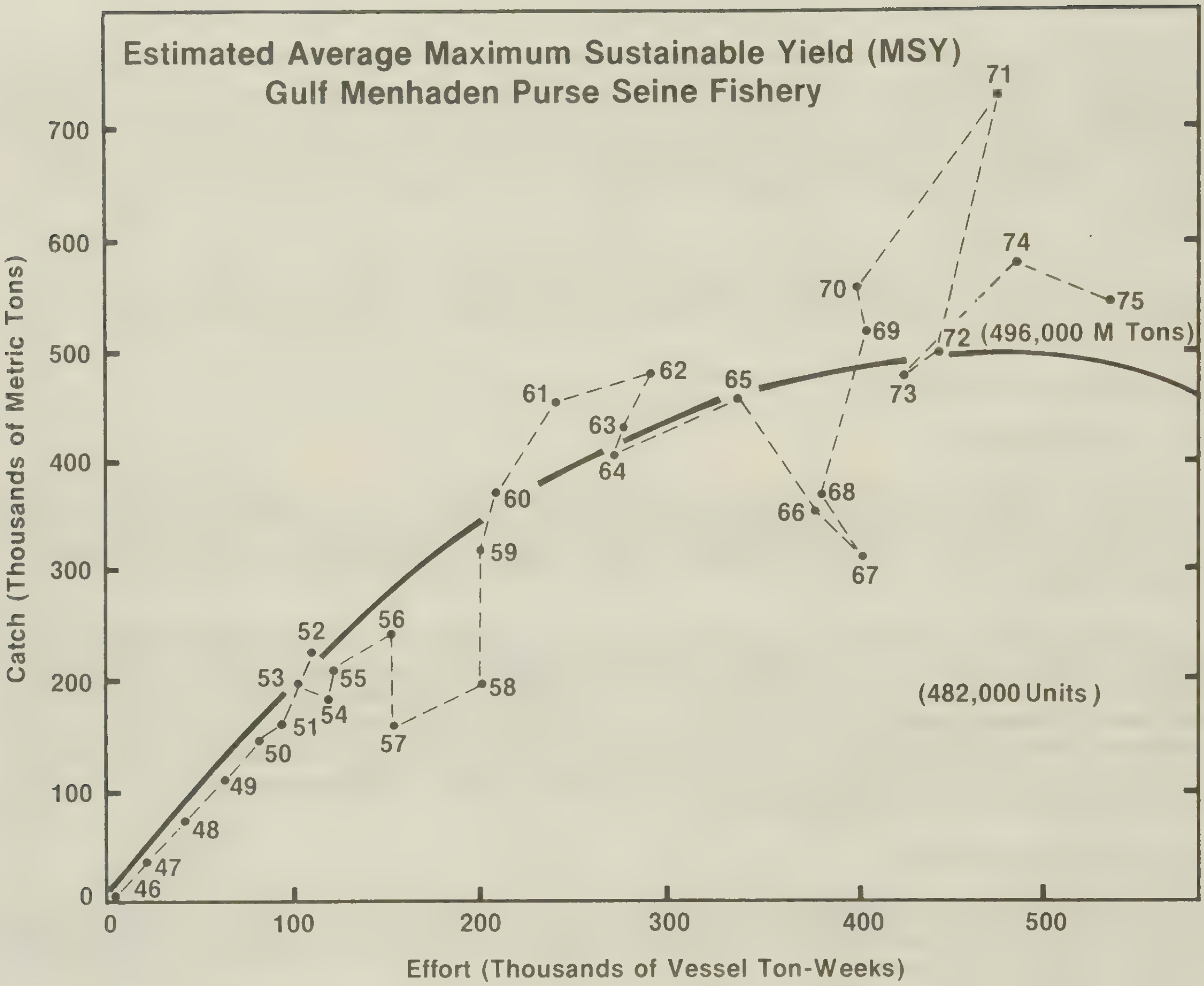

Fig. 1 Estimated average maximum sustainable yield (MSY) Gulf menhaden purse seine fishery

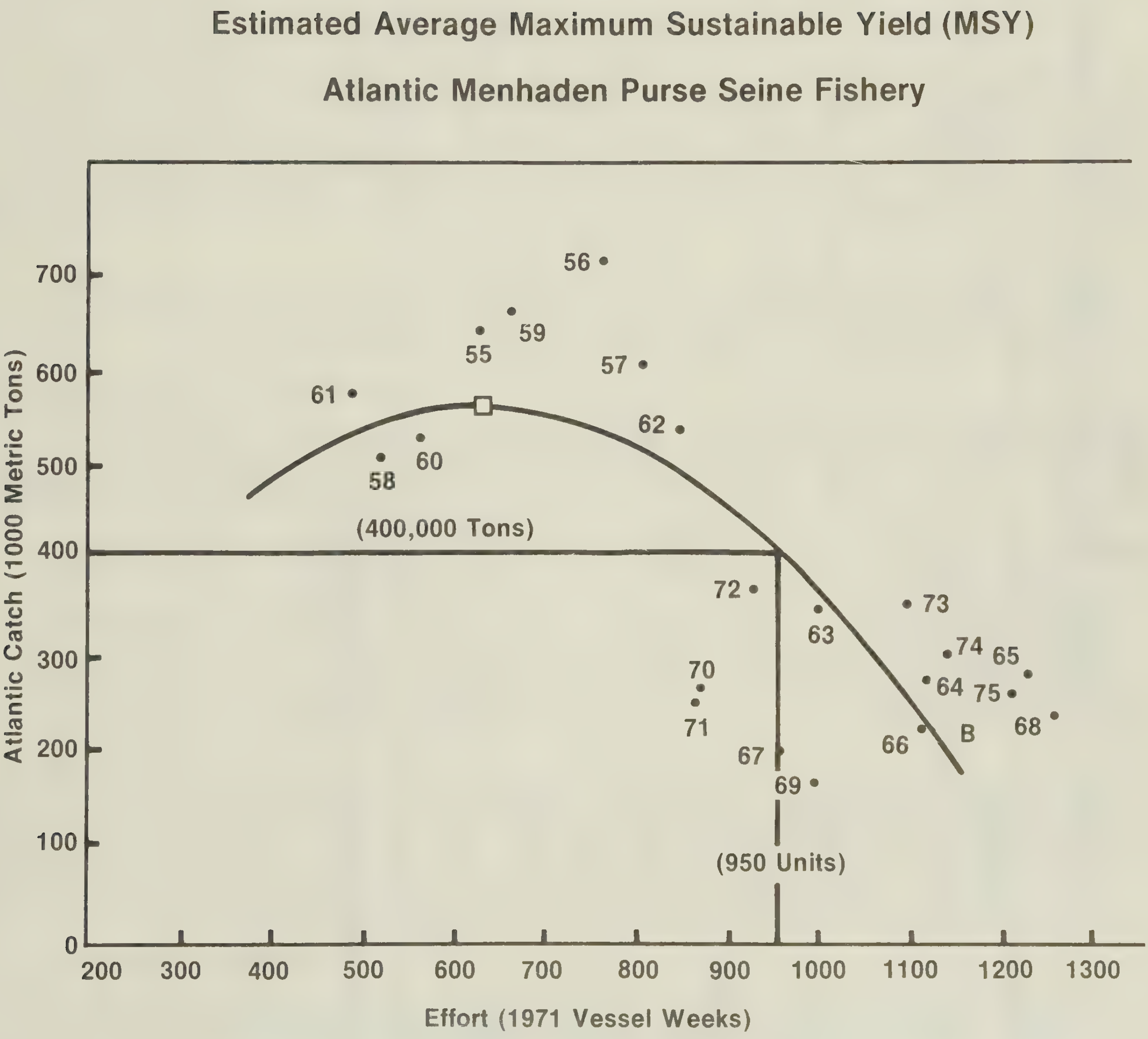

Fig. 2 Estimated average maximum sustainable yield (MSY) Atlantic menhaden purse seine fishery

TABLE IX

Estimates of standing stock and yield for groundfish off South America inshore and offshore areas ('000 t)

	Venezuela	Trinidad	Guyana	Surinam	French Guiana	Total	
km^2							
inshore 0-37 m	17 977	3 200	25 400	43 100	20 200	109 877	201 877
offshore 38-183 m	-	-	20 900	34 400	36 700	92 000	
Standing stock							
inshore 0-37 m	140	23	(148)[a]	193	46	550	1 121
offshore 38-183 m			148	212	211	571	
Yield	35	6	74	101	64	280	
Catch kg/ha potential	19	19	16	13	11	14	

[a] Assume approximately the same as the offshore area

not only near the equilibrium yield curve shown in Fig. 2, but were also near the average maximum level (400 000 t) predicted from the dynamic pool model. Catches of 550 000 t are probably not possible with any level of effort, unless several large year classes enter the fishery. Even then, to achieve large landings would require a mortality rate low enough to allow larger numbers of fish to reach older ages, and hence, greater weight.

Schaaf (1975) estimated a critical level on the "production curve" (B in Fig. 2) and identified it as the biological breakeven point (BBEP). It can be defined as the minimum level at which the fished population can sustain itself. For the Atlantic menhaden, this estimate is 220 000 t and it was obtained from the dynamic pool model by simulating the population through time and finding the maximum mortality rate, and associated yield that it can sustain without declining eventually to zero. As Schaaf indicated, there is a fair amount of uncertainty about its estimation since Atlantic menhaden has shown wide fluctuations in abundance. While application of this estimate should be made with caution, the point does have theoretical importance and could serve as a lower limit for safeguarding the resource from collapse. The optimum age, or the age at which the maximum weight of a year class occurs, is between ages 2 and 3 (Schaaf, 1975). If 17 percent of the harvest consisted of age-3 or older, a maximum equilibrium catch of 400 000 t could be achieved. In 1972, 11 percent of the total catch of 366 000 t landed that year was of these older fish. However, in 1973, 1974 and 1975, about 5 percent or less of the catch was of fish of age-3 and greater.

Continuation of the current harvesting practices will be detrimental to the resource. Implementation of rational management regulations, including a reduction in fishing effort, curtailment of fishing for juvenile menhaden and establishment of a quota is warranted.

5.2 Other Coastal Pelagic Species

There are about 11 other major species of coastal pelagic fish found in the Gulf of Mexico and the southeastern coast of the U.S.A. and utilization of these pelagic stocks is minimal. The species include the following:

Scaled sardine	Harengula pensacolae	Bumper	Chloroscombrus chrysurus
Spanish sardine	Sardinella anchovia	Rough scad	Trachurus lathami
Round herring	Etrumeus teres	Rough scad	Decapterus punctatus
Silver anchovy	Anchoviella eurystole	Thread herring	Opisthonema oglinum
Butterfish	Poronotus triacanthus	Little tuna	Euthynnus alletteratus
Chub mackerel	Scomber japonicus		

The total catch of coastal pelagic species in 1974 amounted to almost 67 000 t, with Venezuela producing almost 56 000 t of Spanish sardines and thread herring. The 1974 U.S. fishery statistics show a catch of 2 600 t of coastal pelagics (butterfish and thread herring) landed valued at U.S.$ 100 000. The estimated potential catch is probably very great, as Bullis and Carpenter (1968) estimate that the standing stock may be close to 7 million t. If this estimate is valid, the resource is essentially untouched.

5.2.1 Status of the stocks

Standing stock estimates in the eastern Gulf of Mexico from egg and larval surveys for round herring and thread herring are provided by Houde (personal communication) and Houde (1973) viz.:

Species	1971-72	1972-73
Round herring	1 400 000	246 000
Thread herring	343 000	311 000

Round herring spawns from October to May in the eastern Gulf, with a spawning peak occurring in the period December to February. Thread herring is confined within an area of 64 km from the shore. Since Houde (1973) never sampled inside the 9 m depth zone in 1971-73, his estimates are conservative. The total potential for the coastal pelagic resource is at present unknown. However, Bullis and Carpenter (1968) estimate standing stocks of 4 800 000 and 1 500 000 t for the Gulf of Mexico and Atlantic seaboard, respectively. Using the yield equation given by Gulland (1971) and assuming $M = 0.5$, the potential yield for those areas would be 1 200 000 and 375 000 t respectively. Wise (1974) estimates an annual harvest of 272 000 t from the Gulf of Mexico. Considering the standing stock estimates for Houde (1973), the potential yield estimated by Wise is rather low.

6. SNAPPER-GROUPER

About 20 species of snappers and groupers are harvested; the red snapper, *Lutjanus campechanus* and red grouper, *Epinephelus morio* are the most important. Total production of snappers and groupers amounted to 44 000 t in 1974. Total snapper production varies considerably and was 21 000 t in 1974, down from 31 000 in 1973, whereas grouper production is relatively stable, around 24 000 t since 1970. The fishing grounds for snappers and groupers include most coastal areas of the region and the oceanic banks. The Campeche Bank area produces 75 percent of the total grouper production and about 10 percent of the total snapper production.

6.1 Status of Stocks

6.1.1 Gulf of Mexico and the southeastern U.S. coastal area

Little information is available on the life history and population dynamics of the exploited fish species. Only crude estimates of standing stocks are available and no estimates of sustainable catch have been made; however, Bullis *et al.* (1971), using data from exploratory surveys, have attempted some estimates. The snapper standing stock in the area is put at 160 000 t and the grouper standing stock for the Western Central Atlantic and Gulf of Mexico is over 110 000 t. The total biomass of snappers and groupers would then be about 270 000 t. Using the potential yield equation given by Gulland (1971) and assuming the natural mortality $M = 0.5$, the potential yield would be about 68 000 t.

The present production of snappers and groupers comes from handline fishing in depths of 55-73 m off reefs, wrecks and oil rigs. However, there is also a sizeable resource along the edge of the continental shelf in the 137-366 m depth zone which could be harvested with bottom setlines and traps. This information is revealed by exploratory fishing in the western Gulf of Mexico in the 183-366 m depth.

The establishment of oil rigs in the Gulf of Mexico has created new fishing grounds for snappers but has brought commercial handlining in direct competition with recreational fishing. Although this competition has not reached a serious stage, the situation is expected to worsen as the two fisheries expand.

6.1.1.1 Groupers

Melo (MS.)investigated the Mexican red grouper fishery, including estimates of growth and mortality rates. He estimated the total mortality rate $Z = .48$, of which natural mortality (M) is in the range of .15-.24. In 1974 the model age group in the catch was two years old, which implies that the young fish are recruited to the adult stock by the age of two years and, at least now, are vulnerable to capture at that age.

Melo's estimates provide all the information necessary to compute the yield per red grouper recruit as a function of age at first capture and fishing mortality rate. The most probable yield isopleths are shown in Figs. 3 and 4 for $M = .15$ and $M = .24$ respectively. The point P in each figure shows the present terms of exploitation. (The present rate of fishing mortality $F = Z - M$ is, by subtraction, in the range .24 - .33.) Both plots show that the yield per recruit could be nearly doubled by increasing the age at first capture from two years to six. Hence the total catch, under proper management, could be increased from the present 19 000 t to perhaps 35 000 t. On the other hand, the number of grouper vessels has been increasing in recent years and Figs. 3 and 4 show that the yield per recruit will decrease if fishing mortality increases and the age at first capture does not.

6.1.1.2 Snappers

The U.S. trawl surveys of 1958-59 showed a standing stock of *Lutjanus campechanus* on Campeche Bank of about 65 000 t which, by the formula presented above, with $M = .2 - .4$, could yield 6 500-13 000 t per year and a yield for all snapper species of 12 000 to 24 000 t. The estimate from Cuban surveys is 29 500 t, with a potential yield of 3 000 to 6 000 t per year and a yield of 22 000 to 44 000 t for all snapper species.

Klima (MS.)estimated the potential yield for Campeche Bank red snapper *Lutjanus campechanus*, using a Schaefer model, to be 4 800 t.

As a group, the estimates of red snapper potential (some of which refer only to *Lutjanus campechanus*) range from 3 000 to 13 000 t. Present catches are only about 3 000 t, nearly all of which are taken by Mexican longline boats, so, despite the crudeness of the estimates of potential, it appears that red snapper catches could be at least doubled to 6 000 t, with total snapper production approaching 20 000 t.

The recent increase in trawling for other species on Campeche Bank might, however, reduce the yield of red snapper to the hook-and-line fishery. Bradley and Bryan (1974) suspected that the incidental catch of juvenile snappers during shrimp trawling in the northern Gulf of Mexico was, in part, responsible for the decline of the hook-and-line fishery off Texas. Shrimp trawling has increased on Campeche Bank, as elsewhere, during the last fifteen years and, since 1962, Cuban and Soviet trawlers have been working the Bank for porgies and grunts. By 1966 they were taking over 30 000 t of various species and, while red snappers are not a significant part of the catch (<5%), even a small fraction of 30 000 t would be a significant removal from the red snapper stocks. Also, some juveniles may be discarded and therefore not reported among the landings.

6.1.2 Caribbean and Bahamas

Klima (MS.) estimated the standing stock of snappers, groupers and related species for the Caribbean, using information given by Kawaguchi (1974), Munro and Thompson (1973) and González-Alberdi (1975). Munro and Thompson (1973) derived a yield curve from data on the catch per canoe per year and the number of canoes per square nautical mile of shelf for different areas along the Jamaican coast. From this, they obtained standing stocks and density estimates which could be related to the catch rate per handline per hour. This ratio and information on catch rates in other areas were used to obtain standing stock estimates for other areas of the Caribbean.

The standing stock of snappers and related species is estimated to be 1 292 000 t and 295 000 t for the Caribbean and Bahamas, respectively. Assuming the natural mortality $M = 0.5$, the author estimated the potential yield using the equation given by Gulland (1971), *viz.*:

(a) potential yield for the Caribbean	323 000 t
(b) potential yield for the Bahamas	73 000 t

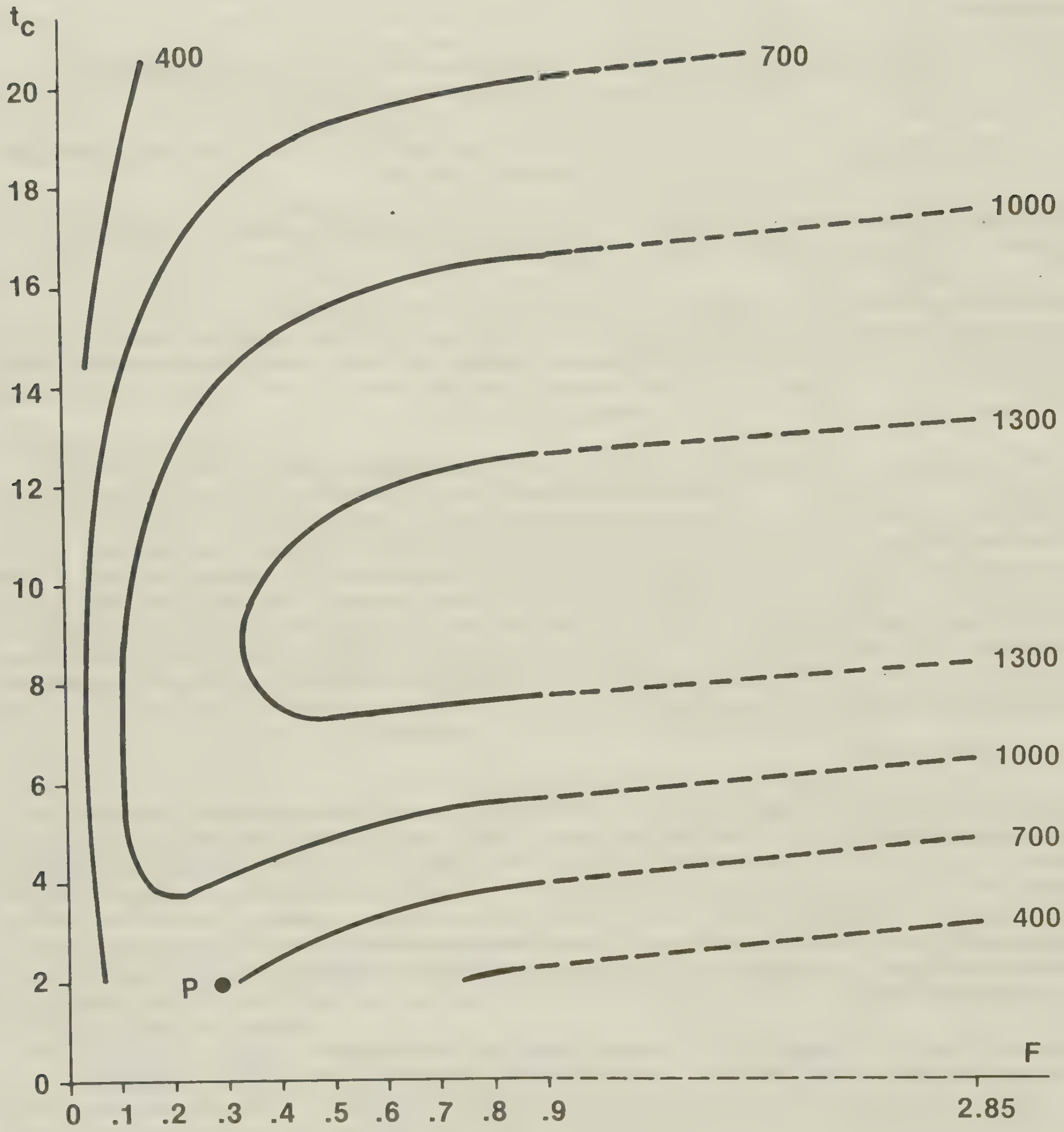

Fig. 3 Yield per recruit of red grouper with M = .15. The point P marks the present fishing mortality rate (F) and age at first capture (t_c). Yields are in grammes per two-year-old recruit)

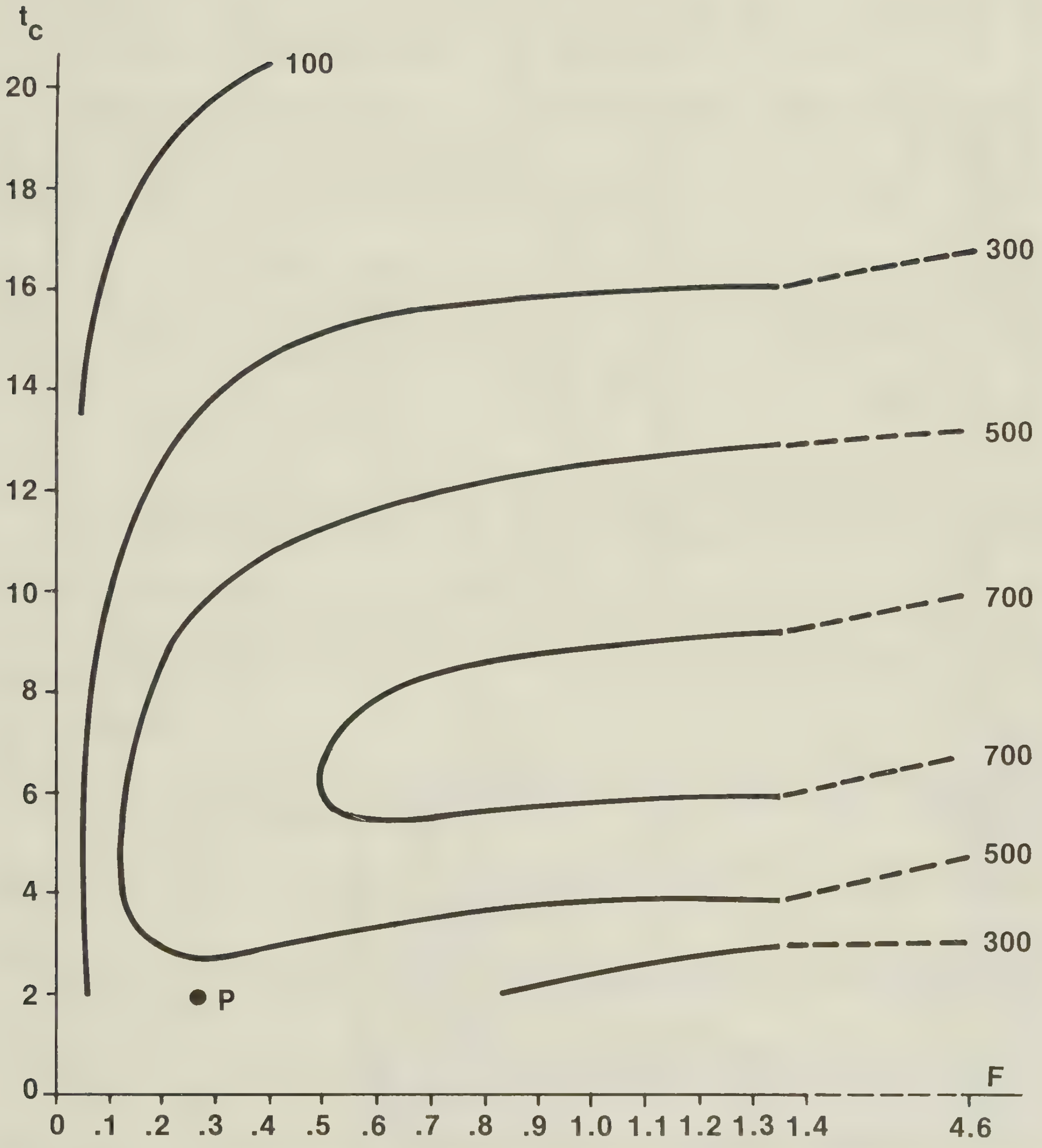

Fig. 4 Yield per recruit of red grouper with M = .24. The point P marks the present fishing mortality rate (F) and age at first capture (t_c). (Yields are in grammes per two-year-old recruit)

TABLE X

Summary estimates of potential in '000 t

	U.S. South Atlantic	U.S. Coast Gulf of Mexico	Campeche Bank	Bahamas	Caribbean	Atlantic Northern South America	Total
Shelf area '000 km^2	175	406	89	190	360	217	1 437
Potential Yield							
Groundfish							
inshore	681	1 187	322	–	–	280	2 470
offshore	25	54	–	–	–	–	79
Coastal pelagics							
menhaden	400[a]	500	–	–	–	–	900
other	375[b]	272[d]–1 200[b]	– [f]	120–240[e]	400–800[e]	150–300[e]	1 317–2 915
Snapper-grouper	34[b/c]	34[c]	55	73	148	175	519
Total	1 515	2 047–2 975	377	193–313	548–948	605–755	5 285–6 883

[a] MSY = 400 000 t for entire Atlantic catches, about 250 000 t

[b] Estimated by Bullis *et al.*, 1971

[c] Half of Bullis estimate for entire region

[d] Wise, 1974 estimate potential at 272 000

[e] Gulland's 1971 estimate

[f] Included in the estimate for the Gulf

7. CONCLUSIONS

The estimated total production for the entire area is between 5.3 and 6.9 million t (Table X). Gulland (1971) estimated the potential for this region to be between 4.0 and 5.7 million t. Total production is about 2.8 million t, with a reported commercial productior of 1.4 million t, an estimated recreational catch of 0.4 million t and about 1.0 million t of fish caught and discarded at sea by the various shrimp fisheries.

Increase in production could be realized in the Gulf of Mexico and along the north coast of South America. Not only could groundfish production be increased but so could production of snapper and groupers and coastal pelagics. A few stocks, such as the Atlantic menhaden, are fully exploited and require management, as increases in fishing effort will not increase fish production.

Although this region offers great promise for increased production, it should, however, be pointed out that most of these resources are usually much more scattered than resources in other regions and are spread over large areas and that the density per unit is, usually, not very high. This characteristic determines the type of fishery which can be developed. Factors which will influence the developments include:

(a) More adequate knowledge concerning the distribution and availability of the stocks.

(b) Adequate techniques by which the stocks can be harvested profitably. This includes the problem whether the fish can be concentrated in, or attracted to, areas where they can be harvested profitably.

(c) Development of an acceptable product and adequate markets.

Development of the groundfish fisheries seems to be the easiest, as harvesting technology is presently available.

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VARIACION ESTACIONAL DEL FITOPLANCTON DE LA BAHIA DE CAMPECHE, MEXICO (1971-72)

por

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Resumen

Se analizaron 203 muestras por el método de Utermöhl colectadas en cuatro épocas del año identificándose 139 especies.

Se describen las comunidades dominantes, su abundancia y distribución para cada época de estudio. Los valores de biomasa se ubicaron entre 10^4 y 10^7 células/litro, encontrándose los números altos a fines de invierno y principios de primavera, y los bajos en otoño. De manera general, se encontró que la mayor biomasa se localiza al margen de la zona costera, y la menor en la región central de la Bahía.

La secuencia general de la sucesión del fitoplancton en orden de abundancia, se puede enmarcar como sigue: en invierno, dominaron Navicula sp., Rhizosolenia setigera, Thalassionema nitzschioides, Nitzschia pungens, Nitzschia closterium, Fitoflageladas, Chaetoceros spp., Rhizosolenia fragilissima y Leptocylindrus danicus; en primavera, le sucedieron incrementos en las poblaciones de Leptocylindrus danicus y Thalassionema nitzschioides, así como la aparición de las especies Skeletonema costatum, Trichodesmium spp., Nitzschia pungens, Chaetoceros coarctatus y Rhizosolenia stolterfothii. En verano se registró un decremento en la biomasa, pero con un mejor desarrollo de Skeletonema costatus y Chaetoceros coarctatus, destacando también Hemiaulus hauckii, Trichodesmium spp., Thalassionema nitzschioides, Rhizosolenia calcar-avis, Fitoflageladas y Nitzschia closterium. Finalmente en otoño se registró un leve florecimiento de Thalassionema nitzschioides, Fitoflageladas, Skeletonema costatum y Rhizosolenia setigera.

Se hacen consideraciones de algunos parámetros ambientales en relación con el fitoplancton. Se incluyen cuatro cuadros que resumen los cambios cualitativos y cuantitativos a través de un ciclo anual.

Abstract

The analysis of 203 samples by the Utermöhl method is given. The samples were collected during four periods in which 139 species were found.

A description of dominant communities, relative abundance, and distribution is given through the year. It was found that biomass values were between 10^4 and 10^7 cells/litre, higher values being found at the end of winter and at the beginning of spring, and low values, in autumn. In general it was found that the highest biomass was located close to the shore line and the lowest in the central area of the Bay.

The general sequence of phytoplankton succession based on the relative abundance was as follows: in winter Navicula sp., Rhizosolenia setigera, Thalassionema nitzschioides. Nitzschia pungens, Nitzschia closterium, phytoflagellates, Chaetoceros spp., Rhizosolenia fragilissima, and Leptocylindrus danicus were dominants; in spring, there was an increase of Leptocylindrus danicus and Thalassionema nitzschioides populations, and also the appearance of Skeletonema costatum, Trichodesmium spp., Nitzschia pungens, Chaetoceros coarctatus, and Rhizosolenia stolterfothii. In summer there was a decrease in biomass, but with good growth of Skeletonema costatum, Chaetoceros coarctatus, Hemiaulus hauckii, Trichodesmium sp., Thalassionema nitzschioides, Rhizosolenia calcar-avis, phytoflagellates, and Nitzschia closterium. Finally in autumn a small peak of Thalassionema nitzschioides, phytoflagellates, Skeletonema costatum, and Rhizosolenia setigera was registered.

Some details of hydrographic parameters in relation to phytoplankton are presented. Also four tables summarizing qualitative and quantitative changes throughout the year are included.

1. INTRODUCCION

En general se puede decir que el fitoplancton del Golfo de México ha sido ampliamente estudiado; Galtsoff (1954), ofrece un resumen de los conocimientos del plancton que hasta la década de los 50 se tenía. Posteriormente se ha avanzado en el conocimiento de las especies, ya que se han abordado aspectos taxonómicos, de distribución y de producción biológica entre los que se pueden mencionar a Curl (1959), Wood (1963), Balech (1967, 1967a, 1967b), Fukase (1967), Saunders y Glenn (1967), Norris (1969), Steidinger (1970, 1973), El-Sayed et al. (1972), Fucik (1974) y Nodar (1974) entre otros. Sin embargo la Bahía de Campeche, a pesar de su enorme importancia por su potencial pesquero, ha sido escasamente estudiada. Aun así existen los trabajos de Schmidt (1873-1904) y Mann (1925) que hacen mención al fitoplancton de esta área. Las investigaciones se inician prácticamente en la última década y los aspectos que hasta hoy se han abordado son todavía muy generales. Entre ellos destacan Khromov (1969), Bessonow et al. (1971), De la Cruz (1971), Santoyo y Signoret (1973, 1975) y Krylow (1974).

Los principales objetivos de esta investigación han sido:

(a) Tener una idea general de los organismos del fitoplancton en la Bahía, su abundancia, distribución y variación estacionales, así como algunas de sus relaciones con el régimen hidrológico;

(b) localización de las áreas de alto contenido en fitoplancton y su variación en las distintas épocas del año.

Este trabajo quedó enmarcado dentro del plan de trabajos hidrobiológicos en el área de influencia de la Laguna de Términos, ubicada en la Bahía de Campeche, dentro de los proyectos para los estudios del CICAR y bajo la dirección del Dr. Alejandro Villalobos.

Los materiales analizados fueron obtenidos a bordo del buque oceanográfico VIRGILIO URIBE (Secretaría de Marina), en que se planearon cuatro cruceros entre el período comprendido entre marzo de 1971 y febrero de 1972, que se hicieron coincidir en cada una de las estaciones del año.

2. AREA DE ESTUDIO

El área muestreada se extiende entre las coordenadas geográficas 18°30'-20°15' N y 90°30'-93°00' O (Fig.1), en la cual se dispusieron 95 estaciones en el proyecto original y proyectadas hasta la isobata de los 183 m, seleccionando de ellas 21 estaciones a criterio del autor.

Los aspectos hidrológicos del área se presentan en detalle por Villalobos y Zamora (1975) y dado que corresponde exactamente a la misma área de estudio y épocas de muestreo que aquí se analizan, lo que enseguida se presenta es una síntesis:

(a) La región de la Bahía de Campeche ubicada frente la Laguna de Términos es una zona altamente dinámica influenciada por los factores propios de la zona costera, así como por los aportes de agua continental. Secundariamente las aguas oceánicas del norte del área, presionan a las masas de agua costera produciendo turbulencias y mezcla;

(b) la oscilación térmica anual varía entre 24 y 29,5°C. La energía calórica se acumula progresivamente en el área costera cuyo caldeamiento persiste durante las calmas con poca modificación por las mareas y sólo se irrumpe por efecto del aporte del agua continental por los ríos Champotón, Grijalva y Frontera que dejan sentir su influencia en ocasiones hasta el borde de la plataforma continental;

(c) el gradiente de salinidad en la superficie va de 37,8 a 35,0 por ciento, siendo los rasgos salinos similares a los de la temperatura, los cuales tienen su origen en las aguas oceánicas, las aguas continentales y las aguas caldeadas, que por evaporación incrementan su salinidad;

(d) las aguas salinas y caldeadas de la costa, incrementan su densidad deslizándose por el lecho marino hasta encontrarse con el agua oceánica que nuevamente las impulsa hacia la superficie produciendo turbulencias;

(e) el contenido de oxígeno disuelto es variable, siendo las aguas continentales que fluyen a la Bahía las que presentan valores altos, excepto cuando llevan abundantes terrigenos.

3. METODOS

Se analizaron un total de 175 muestras colectadas en 21 estaciones (Fig. 1). Las muestras de agua destinadas para el análisis de células del fitoplancton se colectaron en botellas "Nansen" a niveles prefijados (5, 10, 20, 40, 80, 160 m) siempre que la profundidad lo permitiera y se fijaron con una solución de lugol a saturación con acetato de sodio más la adición de gotas de formalina neutralizada. El fitoplancton se analizó cualitativa y cuantitativamente por el método de Utermöhl, analizando en todos los casos volúmenes de 25 cm^3, debido principalmente a la abundancia de sedimentos.

Los resultados cuantitativos obtenidos se expresan en cél/l y su abundancia relativa en por cientos. La cuantificación de algas filamentosas (Trichodesmium y Clorogonium) se determinó por filamentos. Los resultados obtenidos en los análisis cualitativa y cuantitativamente se concentraron en las Tablas I a IV. Con los datos de las cifras de la densidad de fitoplancton se calcularon los valores promedio para cada una de las estaciones de muestreo y para cada época del año, con los cuales se elaboraron los mapas de la Fig. 2, obteniéndose las isoplanctas por interpolación. Asimismo en base a los valores porcentuales de abundancia relativa se calcularon para cada época los valores promedio tanto de densidad, como por grupos taxonómicos y comunidades dominantes (Fig. 3).

Para la identificación taxonómica se recurrió fundamentalmente a claves y descripciones existentes en las obras de Schmidt, 1873-1904; Mann, 1925; Lebour, 1925; Cupp, 1943; Wood, 1954, 1963; Curl, 1959; Brunel, 1962; Hendey, 1964; Balech, 1967, 1967a; Sournia, 1967, 1967a; Saunders y Glen, 1969; y Steindinger y Williams, 1970.

4. FITOPLANCTON CUANTITATIVO

4.1 Primavera

En esta época del año las diatomeas manifestaron la mayor densidad de los componentes del fitoplancton (81 por ciento), el 8,7 por ciento constituido por dinoflageladas. El 5,3 por ciento lo formaron las cianofitas y el 5 por ciento restante estuvo formado por fitoflageladas no identificadas, cocolitofóridas y silicoflageladas (Fig. 3A).

En esta ocasión se observó un claro gradiente en densidad que va de la costa hacia mar abierto, los valores máximos se ubicaron entre 10^5 y 10^6 cél/l. Los valores mínimos se encontraron en la región norte de la Bahía de Campeche con cifras que oscilan por debajo de 10^4 cél/l. La región central de la bahía registró cifras entre 10^4 y $< $ de 10^5 cél/l (Fig. 2). El valor promedio en densidad de organismos fue de 90 460 cél/l.

4.2 Verano

Las diatomeas constituyen una densidad promedio de 59,6 por ciento, siendo las diatomeas centrales las de mayor abundancia, las algas verde-azul estuvieron representadas por el 15,5 por ciento; el 8,1 por ciento lo ocuparon las dinoflageladas. Otras flageladas no identificadas constituyeron el 13,2 por ciento y las clorofitas que aparecieron en esta época registraron el 3 por ciento (Fig. 3A).

TABLA I

Composición, abundancia relativa[1] y densidad[2] del fitoplancton de la Bahía de Campeche, en primavera (28 marzo al 2 de abril 1971)

Estación.	1	7		11		17		26		36	38	43		50	54	64		66		68		70	76		78
Profundidad metros.	5	3	17	3	25	5	15	5	40	10	5	5	30	15	10	5	20	5	20	3	10	5	3	14	5
BACILLARIOPHYCEAE																									
Centricae																									
Bacteriastrum delicatulum	–	–	–	–	–	–	–	–	–	1.8	–	–	–	–	–	–	0.7	–	–	–	–	–	–	–	–
Bacteriastrum hyalinum	–	–	0.2	3.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Biddulphia aurita	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Biddulphia mobiliensis	–	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Biddulphia spp	–	–	–	–	–	–	3.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros affinis	–	–	–	–	–	–	–	–	–	–	–	–	8.5	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros coarctatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	42.8	–	–	–	–
Chaetoceros curvisetus	–	–	–	–	–	–	–	–	–	1.8	–	–	7.6	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros didymus	8.2	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros laevis	–	–	–	–	–	–	–	–	4.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros messanense	–	–	–	–	–	–	–	–	–	5.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros radicans	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros teres	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.5	–	–	–	–	–	–	–	–	–
Chaetoceros spp	–	–	–	11.7	–	19.3	15.1	–	1.5	27.7	–	7.6	3.4	6.3	3.7	–	9.2	–	–	–	–	–	–	–	10.5
Coscinodiscus perforatus	–	–	–	–	–	–	–	–	–	–	–	3.8	–	–	0.7	–	–	–	–	–	–	–	–	–	–
Coscinodiscus radiatus	–	–	–	–	–	3.2	–	–	–	–	–	7.1	3.4	–	–	–	–	–	–	–	–	–	1.7	–	0.11
Cyclotella striata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.5	–	–	–	–	–	–	–
Cymatocira lorenziana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	–
Ditylum sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.9	–	–	–	–	–	2.8	–	–	–	–
Eucampia zodiacus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.4	7.8	–	–	–	–	–
Eucampia sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Guinardia flaccida	–	–	–	–	4.3	–	6.3	–	–	–	–	–	–	–	–	–	14.2	–	3.2	–	–	–	–	–	–
Hemiaulus hauckii	–	–	–	–	–	–	–	–	–	7.4	0.7	–	0.8	–	8.2	–	0.7	–	–	–	–	–	–	–	–
Hemiaulus membranaceus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.5	–	–	–	–	–	–	–
Hemiaulus sinensis	–	–	–	–	–	–	6.3	–	–	–	–	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–
Hemiaulus spp	–	–	–	37.2	–	–	–	–	–	3.7	–	–	–	–	1.4	2.2	5.0	–	–	–	–	–	–	–	–
Leptocylindrus danicus	–	–	–	–	–	–	–	–	–	3.7	–	–	–	–	–	4.5	2.8	–	–	–	–	3.2	67.5	63.6	83.8
Leptocylindrus spp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.77
Melosira sulcata	–	–	–	–	5.4	–	1.2	–	–	–	9.3	–	–	–	1.4	–	–	–	–	–	–	0.4	–	–	–
Rhizosolenia alata f. gracillima	–	–	–	9.8	–	–	8.8	–	–	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia alata f. indica	–	–	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia calcar avis	–	–	–	–	–	–	–	–	–	–	–	–	1.7	–	–	1.5	3.5	–	–	–	–	–	–	–	–
Rhizosolenia fragilissima	–	–	–	–	–	–	–	–	–	9.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia setigera	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia stolterfothii	–	2.5	–	13.7	–	–	–	–	–	7.4	4.2	–	3.8	6.3	–	30.5	15.0	–	–	–	–	–	–	–	–
Rhizosolenia spp	0.5	10.9	1.0	1.9	–	–	–	–	1.5	9.2	0.7	–	–	8.5	5.2	9.1	10.7	9.0	13.0	7.8	17.1	12.0	9.4	7.4	0.55
Skeletonema costatum	–	11.6	57.0	–	–	–	–	–	–	–	–	50.0	9.8	–	–	–	–	–	–	–	–	–	–	–	–
Stephanopyxis palmeriana	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stephanopyxis sp	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–
Thalassiosira sp	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–
Tropidoneis sp	–	–	–	–	–	–	–	–	–	–	0.7	–	–	–	–	–	–	–	1.0	–	–	1.3	–	–	–
No identificadas	–	5.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pennatae																									
Amphora terroris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.6	–	0.9	–	–	–
Amphora sp	2.3	0.6	2.4	1.9	18.6	–	–	–	1.5	1.8	7.8	–	0.4	–	1.4	0.7	–	–	2.1	–	–	3.7	0.8	2.4	0.2
Bacillaria paradoxa	–	–	–	–	–	–	–	–	–	–	–	–	11.9	–	–	–	–	–	–	–	–	–	–	–	–
Cocconeis sp	–	–	–	1.9	–	–	–	–	–	–	1.5	–	–	–	2.9	–	–	4.5	–	–	–	1.3	2.5	2.4	–
Dimerogramma marinum	–	–	–	–	–	–	–	–	–	–	5.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diploneis bombus	–	–	1.3	–	15.3	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diploneis weissflogii	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–
Diploneis sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.7	–	–	2.6	–	–	–	–	–
Gyrosigma sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mastogloia spp	–	–	1.3	–	5.4	–	2.5	–	–	1.8	–	–	0.4	–	–	–	–	–	2.1	–	–	–	0.8	1.6	–
Navicula wawrikae	–	–	–	–	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Navicula spp	–	–	0.5	1.9	2.1	6.4	2.5	11.7	4.6	–	5.8	–	–	2.1	1.4	2.2	–	9.0	3.2	–	–	2.7	1.7	2.4	0.55
Nitzschia acicularis	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1	–	–	–	–	–	–	–	0.9	–	4.9	–
Nitzschia closterium	5.2	0.6	0.5	1.9	–	3.2	8.2	–	6.2	–	3.1	11.5	0.8	10.6	11.1	3.8	4.2	–	5.4	10.5	2.8	7.4	1.7	1.6	0.81
Nitzschia panduriformis	–	–	0.2	–	5.4	–	1.2	–	–	–	1.5	–	–	–	–	–	0.7	–	2.1	–	2.8	–	–	–	–
Nitzschia pungens	–	11.6	0.5	–	–	–	–	–	43.7	–	–	3.8	10.2	–	–	–	2.8	4.5	1.0	–	–	–	–	–	0.3
Nitzschia sigma	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–
Nitzschia silicula	–	–	–	–	–	–	–	–	–	–	0.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia spp	–	2.5	0.2	–	–	3.2	8.8	5.8	1.5	–	1.1	7.6	1.7	17.0	2.2	10.6	3.5	18.1	4.3	2.6	–	0.9	0.8	2.4	–
Plagiogramma spp	4.1	–	–	–	–	–	–	–	–	–	1.5	–	–	–	–	–	–	–	–	10.5	–	–	–	–	–
Pleurosigma elongatum	–	–	–	–	1.0	–	–	–	–	–	–	–	–	–	–	0.7	–	–	–	–	–	–	–	–	–
Pleurosigma normanii	–	–	0.2	–	3.2	–	–	–	–	–	–	–	–	–	0.7	–	–	–	–	5.2	–	–	–	–	0.11
Pleurosigma spp	0.5	–	–	–	–	–	–	–	–	1.8	–	–	0.8	–	–	–	4.2	–	1.0	10.5	–	–	–	–	–
Surirella spp	–	–	1.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Synedra ulna	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thalassionema nitzschioides	70.5	1.2	21.7	–	14.2	12.9	7.5	5.8	12.5	3.7	45.3	–	13.6	–	305	9.9	11.4	9.0	11.9	7.8	17.1	3.7	–	–	–
Thalassiothrix frauenfeldii	0.5	4.5	–	–	–	–	3.7	–	3.1	–	4.6	–	0.1	2.1	0.7	5.3	5.7	–	8.6	–	–	6.0	–	–	–
Thalassiothrix sp	–	–	–	–	2.1	–	–	–	–	–	0.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
No identificadas	2.3	–	–	–	14.2	12.9	5.0	–	7.8	–	1.7	3.8	0.4	4.2	12.6	–	–	4.5	–	5.2	–	504	5.9	6.6	1.7
DINOPHYCEAE																									
Ceratium fusus	–	–	–	–	–	3.2	–	–	–	–	–	–	–	–	–	–	0.7	–	–	–	2.8	–	–	–	–
Ceratium furca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ceratium spp	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–
Dinophysis caudata	–	–	–	–	–	–	–	–	–	–	–	3.8	–	–	–	–	–	–	–	–	–	–	–	–	–
Exuviaella sp	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	2.1	–	2.8	–	–	–	–
Gyrodinium spp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.0	–	–	–	–	–	–	–	–	–
Gymnodinium sp	–	–	–	–	–	–	–	17.6	1.5	–	1.9	–	1.2	25.5	2.2	–	–	13.6	18.4	13.1	–	2.7	5.1	2.4	0.11
Peridiniopsis sp	–	–	–	–	–	–	5.0	–	–	–	–	–	–	–	–	2.2	–	–	5.4	2.6	–	–	–	–	–
Peridinium depressum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Peridinium sp	–	0.6	0.2	–	–	–	2.5	–	3.1	–	–	–	–	–	–	–	2.1	–	2.1	–	2.8	1.8	0.8	–	0.11
Prorocentrum micans	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pyrophacus sp	–	–	–	–	–	–	–	–	–	–	0.7	–	–	–	–	–	–	–	–	2.6	–	–	–	–	–
Dinoflageladas desnudas	2.3	37.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.6	–	–	–	–	–
Dinoflageladas tecadas	–	–	0.8	3.9	–	9.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CYANOPHYCEAE																									
Trichodesmium spp	–	5.1	–	1.9	–	–	–	58.8	3.1	7.4	–	–	–	–	3.7	–	–	18.8	–	2.6	–	–	0.8	–	–
Cianofitas Chroococcales	0.5	–	0.2	–	–	9.6	3.7	–	1.5	–	–	–	–	–	–	1.5	–	–	2.1	–	5.7	–	–	–	–
Cianofitas Hormogonales	–	–	–	–	–	–	–	–	–	–	–	–	–	6.3	–	–	–	–	–	–	–	–	–	–	–
SILICOFLAGELLATAE																									
Dictyocha spp	–	–	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
COCCOLITHINEAE																									
Coccolithus sp	–	–	–	–	1.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
No identificadas	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
LITOFLAGELADAS																									
No identificadas	1.1	0.6	–	1.9	–	–	–	–	1.5	1.8	–	–	–	–	0.7	0.7	1.4	–	2.1	5.2	–	–	–	–	–
ADDENDA																									
Chaetoceros lorenzianus	–	–	–	–	–	–	–	–	–	–	–	–	10.6	–	–	9.1	–	–	2.1	–	–	–	–	–	–
Coscinodiscus spp	–	–	7.0	–	5.4	–	3.7	–	–	–	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–	0.11
Cyclotella sp	–	–	–	–	1.09	–	1.2	–	–	–	–	–	3.4	–	–	–	–	–	–	–	–	–	–	–	–
Dictyocha fibula	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dinophysis sp	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–
Gymnodinium spp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gyrosigma balticum	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Melosira sp	–	–	–	–	–	–	–	–	–	–	0.7	–	–	–	1.49	–	–	–	–	–	–	–	–	0.8	–
Rhizosolenia acuminata ?	–	–	–	–	–	16.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia stiliformis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.8	–
Thalassionema spp	1.17	2.5	–	7.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
DENSIDAD DE FITOPLANCTON																									
Células/litro x 1,000	170	31	146.8	10.2	18.2	6.2	15.8	3.4	12.8	10.8	256	6.5	117	9.4	134	52.4	56	4.4	18.4	7.6	7	216	23.4	24.2	904

[1] La abundancia relativa de esta referida en porcientos

[2] La densidad se expresa en células/litro

TABLA II

Composición, abundancia relativa1/ y densidad2/ del fitoplancton de la Bahía de Campeche en verano (7 al 15 agosto 1972)

Estación.	1	7		11		17			26			31			36			38	50			54	64			66	68		70	76		78	80					84				90			92		
Profundidad metros.	5	5	10	5	10	5	10	20	5	10	20	5	10	20	5	11	16	7	5	10	20	5	5	10	20	20	5	10	5	5	10	5	5	10	20	40	80	5	10	20	80	5	20	40	5	80	160
BACILLARIOPHYCEAE																																															
Centricae																																															
Actinoptychus heptactis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–
Actinoptychus sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bacteriastrum elongatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bacteriastrum sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros coarctatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	18.6	29.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros constrictum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros debilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros laevis	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros lorenzianus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.6	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros pendulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4	–	–	–	–	4.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros radicans	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.8	5.2	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros teres	–	0.08	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12.9	–	1.2	3.5	–	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros spp	–	0.08	–	–	–	–	–	–	–	–	–	–	–	–	–	27.2	15.4	–	0.5	–	4.2	50.0	4.8	16.1	26.5	5.3	–	1.6	4.1	4.0	–	–	–	–	–	–	–	18.1	–	5.5	–	–	–	–	–	–	–
Corethron criophylum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corethron sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Climacodium frauenfeldianum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coscinodiscus radiatus	–	0.17	4.54	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	0.9	2.6	–	–	–	–	–	–	–	–	–	–	–
Coscinodiscus spp	–	–	–	–	–	–	7.1	–	–	–	–	–	–	–	–	–	1.4	–	1.7	25.0	–	–	1.6	–	–	1.7	0.15	–	3.5	–	–	–	3.6	–	–	2.6	–	–	–	–	–	–	–	–	–	–	–
Cyclotella striata	–	–	9.0	–	–	–	–	–	–	–	13.3	–	–	–	–	–	–	–	0.5	–	–	–	1.6	–	–	–	0.4	0.3	–	–	9.0	0.24	27.2	10.4	10.0	5.2	–	–	–	–	56.4	2.3	–	–	12.5	–	2.8
Ditylum brightwellii	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diploneis bombus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	–	–	–	–	–	–	–	–	–	–	3.1	–	–	–	15.3	–	–	–	–	–	–
Diploneis sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	–	–	–	4.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eucampia zodiacus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.3	–	–	–	–	–	–	–	–	–	–	–	–	–
Eucampia sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Guinardia flaccida	–	–	4.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	–	0.49	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hemiaulus haurckii	–	–	–	28.5	20.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	68.9	38.8	1.1	–	–	55.9	–	–	–	–	–	–	–	–	5.1	6.9	–	–	–	–	–
Hemiaulus membranaceus	–	–	–	–	20.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hemiaulus spp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.6	–	–	–	4.2	13.3	–	–	–	19.6	–	2.3	–	–	–	–	–	–	–	4.6	–	–	–	–	–
Leptocylindrus danicus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8.4	–	–	–	3.6	–	–	17.6	1.8	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leptocylindrus sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Melosira sulcata	–	–	–	–	–	–	–	–	5.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.47	–	1.1	–	–	–	–	–	–	5.2	–	–	–	–	–	–	–	–	–	–	–
Melosira sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia alata f. indica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.15	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia alata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20.0	–	–	–	–	–	1.4	3.0	–	6.9	13.7	–	8.0	–	–	–	–	–	5.2	–	–	–	5.5	–	–	–	–	–	–	–
Rhizosolenia acuminata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.6	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia bergonii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	0.15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia calcar avis	–	–	–	–	2.5	–	–	–	–	–	–	16.6	–	–	–	–	–	–	–	–	–	25.0	–	–	1.7	1.7	–	3.1	–	44.0	9.0	–	–	–	–	2.6	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia fragilissima	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.49	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia hebetata f. semispina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.2	1.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia imbricata v. shrubsolei	–	–	–	–	–	–	–	–	–	11.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4	–	2.3	–	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia robusta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia setigera	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.5	–	–	2.9	6.0	–	0.7	13.5	–	–	–	0.24	1.8	–	–	–	6.2	–	–	–	–	–	–	–	–	–	–
Rhizosolenia stolterfothii	–	–	4.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.15	1.3	–	–	9.0	2.4	–	–	–	7.8	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia spp	–	0.08	–	–	–	–	–	–	–	–	–	–	1.4	–	1.1	–	–	–	–	–	–	–	–	–	4.2	–	–	–	–	–	–	4.4	–	0.9	–	–	–	–	–	–	–	–	–	3.5	–	–	–
Skeletonema costatum	–	75.8	–	–	17.5	–	–	–	–	–	–	–	–	–	–	–	–	–	10.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	37.5	–	–	–	–	–	–	–	62.5	–	–
Skeletonema sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stephanopyxis turris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
No identificadas	–	–	–	–	–	–	–	4.6	–	22.2	–	16.6	3.5	–	–	–	–	–	–	–	0.6	12.5	–	–	–	–	–	–	–	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–
Pennatae																																															
Amphora marina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphora spp	–	0.08	–	–	–	–	–	3.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.3	–	–	2.9	–	–	–	–	4.6	–	–	18.7	–	–	–	2.5	–	–	–	–	–	–
Amphiprora gigantea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphiprora paludosa	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphiprora sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cocconeis sp	–	–	–	–	2.5	–	–	–	17.6	–	33.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.16	1.1	–	–	0.74	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Grammatophora oceanica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Grammatophora sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.6	–	–	7.1	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gyrosigma sp	–	–	–	–	–	–	–	2.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mastogloia sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Navicula wawrikae	–	–	–	–	–	–	–	–	–	–	–	–	–	4.3	1.1	–	–	–	–	–	0.6	–	–	–	0.6	–	–	–	–	4.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Navicula spp	–	–	–	–	–	–	–	–	–	11.1	–	–	1.4	4.3	–	–	–	40.0	–	–	–	–	–	1.4	–	1.7	0.7	–	1.7	8.0	9.0	0.49	–	–	0.9	5.2	3.1	–	–	–	–	–	–	–	–	–	–
Nitzschia closterium	–	0.4	4.5	–	–	100.0	57.1	46.5	–	–	–	–	–	–	–	–	33.8	20.0	0.5	–	11.0	–	–	4.4	13.2	–	4.2	2.4	1.1	–	–	1.9	–	–	–	–	3.1	–	–	–	–	–	–	–	–	–	–
Nitzschia pacifica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8	–	–	–	–	–	–	25.0	–	–	–	–	–	–	18.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia panduriformis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.15	–	–	–	–	–	–	–	–	–	6.2	–	–	–	–	–	–	–	–	–	2.8
Nitzschia pungens	–	–	–	–	–	–	7.1	–	–	–	–	–	–	–	–	–	–	–	–	–	1.2	–	–	–	9.0	–	2.0	1.3	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia sigma	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia spp	20.0	0.2	9.0	–	–	–	–	2.3	11.7	22.2	–	–	–	–	–	6.8	7.0	–	0.5	–	–	–	1.6	1.4	1.2	–	0.7	0.32	25.0	4.0	–	5.7	–	–	–	2.6	–	–	–	–	5.1	–	–	–	–	–	–
Plagiogramma sp	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleurosigma angulatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleurosigma sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	3.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Synedra sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thalassionema nitzschioides	–	2.3	27.2	–	–	–	–	1.1	–	–	–	–	–	–	3.4	2.2	11.2	–	1.1	–	58.2	–	–	–	3.0	8.9	3.0	3.9	10.7	–	–	–	34.5	34.8	39.0	7.8	3.1	–	–	–	5.1	–	–	–	–	–	–
Thalassionema sp	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.6	–	1.8	–	–	–	–	–	–	–	3.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thalassiothrix frauenfeldii	–	–	–	–	10.0	–	7.1	–	11.7	–	–	–	1.4	–	–	–	–	–	0.5	16.6	7.3	12.5	12.9	–	1.2	5.3	–	2.2	–	–	9.0	–	3.6	6.9	7.4	2.6	–	–	–	11.1	2.5	–	–	7.1	–	–	–
No identificadas	–	–	–	–	–	–	–	–	–	–	–	–	3.5	–	–	18.1	–	–	–	–	0.6	–	–	5.8	–	39.2	–	–	–	–	–	–	–	–	2.7	2.6	3.1	–	–	–	–	–	7.5	3.5	–	–	18.2
DINOPHYCEAE																																															
Ceratium furca	20.0	–	4.5	–	–	–	–	–	–	–	–	–	–	4.3	–	–	–	–	–	–	–	–	1.6	–	–	–	–	–	–	4.0	–	–	7.2	3.4	–	–	–	–	–	–	–	–	–	–	–	–	–
Ceratium fusus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ceratium teres	–	–	–	–	–	–	–	–	–	–	–	16.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ceratium sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Goniaulax sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gyrodinium sp	–	–	–	–	–	–	–	1.1	–	–	13.3	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	0.31	–	–	–	–	–	–	–	–	–	–	9.0	–	–	–	–	–	3.5	–	–	–
Oxytoxum sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.4	–	–	–	–	–	5.5	–	–	–	–	–	–	–
Peridinium depressum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Peridinium scutellum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Prorocentrum micans	–	–	–	–	–	–	–	2.3	–	–	–	–	–	–	–	–	2.8	–	–	8.3	–	–	–	–	–	–	0.3	–	–	–	–	–	–	–	–	–	3.1	–	–	–	–	–	–	–	–	–	–
Prorocentrum triestinum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.5	–	–	–	–
Prorocentrum spp	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.0	–	–	–	–
Dinoflageladas tecadas	–	0.2	4.5	–	–	–	–	–	–	11.1	6.6	–	1.4	–	–	4.5	–	–	0.5	–	–	–	1.61	1.4	–	–	–	–	1.7	–	–	–	1.8	–	–	2.6	–	–	–	–	–	–	2.5	–	–	–	–
Dinoflageladas desnudas	–	–	13.6	–	–	–	–	1.1	5.8	–	–	–	1.4	–	–	6.8	1.4	–	–	–	–	–	–	–	4.2	–	–	–	0.5	–	–	1.2	–	–	–	–	–	–	–	–	5.1	16.2	–	14.2	–	–	–
CYANOPHYACEAE																																															
Chroococcaceae	–	1.4	4.5	–	2.5	–	14.2	11.6	–	–	–	–	7.8	21.7	2.3	–	–	–	0.5	–	1.8	–	–	–	–	–	0.6	–	38.6	12.0	27.2	–	–	–	2.7	–	–	–	–	27.7	–	44.1	22.5	10.7	–	–	–
Hormogonales	–	–	–	28.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Merismopedia sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.6	–	–	–	–	–	–	–	–	–	–	–	–	–
Phormidium sp	–	–	–	–	–	–	–	–	–	–	–	–	0.71	–	–	–	–	–	60.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8
Trichodesmium spp	60.0	–	–	–	17.5	–	–	11.6	–	–	–	–	3.5	–	69.7	–	–	–	–	–	–	–	48.3	–	–	–	–	–	–	–	–	–	–	11.6	2.7	–	–	–	–	16.6	–	–	–	–	25.0	–	4.2
No identificadas	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CHLOROPHYCEAE																																															
Chlorella sp	–	–	–	–	–	–	–	–	–	–	–	–	–	21.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	23.9
Chlorogonium sp	–	12.9	–	–	–	–	–	4.6	–	–	–	–	–	21.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
No identificadas	–	–	–	–	–	–	–	–	–	–	–	–	40.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SILICOFLAGELLATAE																																															
Dictyocha fibula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.7	–	0.6	–	–	–	–	–	–	–	–	–	–	–	1.8	1.1	1.8	–	–	–	–	–	–	–	–	–	–	–	–
Dictyocha octonaria	–	–	4.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dictyocha sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
FITOFLAGELADAS																																															
No identificadas	–	–	4.5	–	2.5	–	–	3.4	47.0	22.2	33.3	33.3	30.0	17.3	2.3	–	1.4	20.0	–	–	2.4	–	–	–	6.6	1.7	2.3	2.9	2.3	4.0	9.0	2.2	–	4.6	9.0	10.5	12.5	72.7	–	5.5	2.5	25.5	17.5	53.5	–	100.0	30.91
ADDENDA																																															
Chaetoceros didymus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11.1	–	–	–	–	–	–	–
Corethron sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyclotella sp	–	–	–	–	–	–	–	–	–	–	–	–	3.5	–	–	–	–	–	–	50.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.2	5.2	–	–	–	–	–	–	10.0	–	–	–	–
Exuviaella sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gymnodinium spp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	4.8	–	–	–	–	–	–	–	–	–	–	1.1	2.7	10.9	–	–	–	5.5	–	–	22.5	–	–	–	4.9
Nitzschia acicularis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Peridinium spp	–	–	–	–	–	–	7.1	1.6	–	–	–	16.6	2.8	–	–	–	–	–	–	–	–	–	–	2.9	–	–	–	–	–	–	–	–	–	3.4	3.6	5.2	–	–	–	5.5	–	–	5.0	–	–	–	–
Rhizosolenia delicatula	–	4.0	42.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spirulina sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	–	–	–
Thalassiosira sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.6	2.6	–	–	–	–	–	–	–	–	–	–	2.8
DENSIDAD DE FITOPLANCTON																																															
Células/litro x 1,000	0.5	700	2.2	1.4	4	0.2	1.4	8.2	1.7	1.8	1.5	0.6	14	17.6	8.6	1.7	2.8	0.5	34	1.0	16.3	0.8	6.2	17	6.6	5.6	631	612	67.2	2.5	2.2	402	5.5	8.6	11	3.8	3.2	2.2	0	7.8	3.9	4.3	4	2.8	1.6	0.2	7.1

1/ La abundancia relativa está referida en porcientos

2/ La densidad se expresa en células/litro

TABLA III

Composición, abundancia relativa[1] y densidad[2] del fitoplancton de la Bahía de Campeche en otono (21 al 26 septiembre 1971)

Estación	1		7		11			17		26				31		36	38		43			50			54	64			66			68		70		76	78	80			84			90					92					
Profundidad metros	5	10	5	10	5	10	20	5	10	5	10	20	40	10	20	10	5	10	5	10	20	5	10	20	5	5	10	20	5	10	20	5	10	5	7	5	5	5	10	20	5	80	160	5	10	20	40	80	5	10	20	40	80	130
BACILLARIOPHYCEAE																																																						
Centricae																																																						
Bacteriastrum elongatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bacteriastrum delicatulum	0.22	2.0	—	—	—	6.2	—	—	3.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.1	11.7	—	—	—	—	0.9	—	—	—	—	—	—	0.86	—	—	6.6	—	—	—	—	4.8	—	—	—	—	—
Biddulphia sinensis	—	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaetoceros affinis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.8	—	—	—	—	—	—	—	—	—	12.9	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaetoceros laevis	—	1.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.5	—	—	—	—	2.9	—	—	7.6	—	—	—	—	—
Chaetoceros lorenzianus	—	—	—	—	—	—	—	—	—	—	—	—	—	2.6	9.5	—	—	—	—	2.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—	—	—	—	11.7	1.4	—	—	—	4.5	—	—	—	—
Chaetoceros radicans	—	—	—	—	—	—	—	—	—	—	—	—	—	0.65	—	—	—	—	—	1.3	—	—	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.5	—	—	—	—
Chaetoceros spp	3.6	42.5	—	—	—	16.7	—	—	34.6	15.0	—	—	30.0	—	—	—	21.9	—	10.1	—	3.7	9.2	—	—	—	—	—	17.4	—	—	3.7	—	—	54.0	16.1	—	0.6	3.1	—	—	4.31	—	—	6.6	—	—	—	—	2.88	—	—	—	—	—
Corethron criophylum	—	1.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Corethron sp	—	—	4.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.5	—	—	—	—	—	3.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coscinodiscus perforatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coscinodiscus spp	—	0.5	2.0	—	14.2	—	—	—	3.8	—	—	—	3.3	—	—	2.0	—	—	—	—	—	—	—	—	—	—	—	1.1	—	—	—	—	—	—	4.4	—	—	—	—	—	—	—	—	6.6	—	—	—	—	—	—	—	—	25.0	—
Cyclotella sp	—	—	—	—	—	—	—	3.1	—	5.0	—	—	—	—	—	10.0	0.95	22.7	—	—	0.53	—	—	6.2	—	—	—	—	—	—	2.8	—	—	2.7	—	—	1.0	—	—	—	—	—	—	—	—	—	5.8	—	—	—	—	—	—	—
Ditylum sp	—	—	—	—	—	12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.6	—	—	—	—	—	—	—	—	—	—	—	0.96	—	—	—	—	—
Eucampia zodiacus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Guinardia flaccida	0.22	1.5	6.0	7.6	—	—	6.6	3.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.59	—	—	—	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hemiaulus hauckii	0.11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.0	4.7	0.53	—	—	—	—	—	—	2.3	—	—	—	—	—	8.1	—	—	0.6	—	—	—	1.7	—	—	—	—	1.4	—	—	1.92	—	—	—	—	—
Hemiaulus membranaceus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leptocylindrus danicus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Melosira sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizosolenia alata f. gracillima	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizosolenia alata	—	—	—	—	—	—	—	—	—	—	—	—	—	0.48	—	—	—	—	1.0	2.7	7.4	—	—	—	—	—	—	—	—	3.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.9	—	—	—	3.0	—	—	—	—
Rhizosolenia calcar-avis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.6	—	—	—	—	1.92	—	—	—	—	—
Rhizosolenia delicatula	—	—	—	—	71.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizosolenia fragilissima	0.90	—	—	—	—	—	—	9.3	7.6	—	—	—	—	—	—	—	—	—	47.8	51.0	77.5	80.7	23.2	—	—	—	—	23.2	—	12.1	—	—	—	0.9	—	99.9	1.3	—	—	—	6.8	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizosolenia imbricata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.7	—	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizosolenia setigera	—	1.0	—	—	—	37.5	—	—	—	—	—	8.3	3.3	0.65	4.7	—	7.6	—	—	—	—	—	—	—	—	1.76	—	9.3	—	3.0	20.7	—	—	7.2	7.3	—	0.3	6.2	9.6	21.2	25.8	—	—	—	32.3	32.3	11.76	—	38.4	50.0	4.4	17.6	—	—
Rhizosolenia stiliformis	—	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.6	—	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhizosolenia stolterfothii	0.34	0.5	—	—	—	—	—	15.6	—	—	—	—	—	—	—	—	—	—	1.0	2.0	0.53	—	2.3	—	—	—	—	—	—	—	0.94	—	—	6.3	23.5	0.03	2.0	—	—	—	1.7	—	—	—	—	2.9	—	—	11.5	—	—	—	—	—
Rhizosolenia spp	—	—	2.0	—	—	—	—	3.1	—	—	—	8.3	—	—	—	—	—	—	—	—	—	0.7	2.3	—	8.3	0.59	—	2.3	—	—	—	—	—	0.90	—	—	0.6	—	3.6	—	—	—	—	20.0	—	—	—	—	—	—	0.56	—	—	—
Skeletonema costatum	—	—	—	—	—	—	—	—	—	—	—	—	26.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.8	—	—	—	—	—	—	75.0	19.5	17.5	—	—	—	—	—	—	47.0	—	2.8	—	2.80	—	—	—
Thalassiosira sp	—	—	—	—	—	—	—	—	—	—	7.6	—	—	—	—	—	—	—	—	—	—	—	6.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.9	—	—	—	—	—	—	1.4	—	—	—	—	—	—	—	—
No identificadas	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pennatae																																																						
Amphora spp	0.1	0.5	—	—	—	—	—	—	3.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.59	—	—	—	—	4.7	—	—	—	—	0.02	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cocconeis sp	—	—	6.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Navicula sawrikae	—	—	—	—	—	—	13.3	—	—	—	—	—	—	—	—	—	—	—	4.2	0.68	—	—	6.9	—	—	—	—	—	11.7	3.0	—	—	—	0.9	—	—	—	—	—	1.2	—	—	—	—	—	—	—	—	0.96	—	—	—	—	—
Navicula spp	0.11	—	2.0	—	—	6.2	—	3.1	—	—	—	—	—	—	—	2.0	0.95	—	0.53	0.68	1.0	0.7	—	—	—	0.59	10.5	26.7	5.8	3.0	2.8	—	—	—	1.4	—	0.3	6.2	—	—	1.7	—	—	—	—	—	—	—	—	—	0.56	—	—	40.0
Nitzschia acicularis	—	—	—	—	—	—	6.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nitzschia closterium	—	0.5	—	—	—	—	—	—	—	—	—	8.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nitzschia pungens	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.96	—	—	—	—	—
Nitzschia spp	—	—	—	—	—	—	—	3.1	—	15.0	—	—	—	0.65	—	2.0	—	—	—	—	0.53	—	—	—	—	0.59	—	5.8	—	—	1.8	—	7.6	—	—	—	—	—	5.7	—	0.86	—	—	6.6	—	—	—	—	—	—	—	—	—	—
Plagiogramma sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pleurosigma sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Surirella fastuosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.59	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thalassionema nitzschioides	0.56	25.0	60.0	61.5	—	—	—	—	—	—	—	—	—	—	—	12.0	—	4.5	3.1	2.0	—	—	—	—	—	92.2	—	—	—	—	6.6	—	—	13.5	38.2	—	78.7	6.2	23.0	22.5	34.4	—	—	20.0	—	20.5	23.5	—	16.3	22.7	—	—	—	—
Thalassionema sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	26.0	45.7	36.3	—	—	0.53	—	2.3	12.5	—	—	—	—	—	—	—	—	61.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thalassiothrix frauenfeldii	—	—	—	—	—	—	—	—	—	—	—	—	13.3	—	—	—	—	—	1.0	—	0.53	—	—	—	—	1.19	—	—	—	—	22.6	—	—	—	—	—	6.8	—	—	—	—	—	—	—	—	—	—	—	2.88	—	—	—	25.0	—
No identificadas	0.11	—	—	—	—	6.2	—	—	—	5.0	—	—	—	—	—	—	—	9.0	—	—	—	—	2.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.9	—	1.68	—	—	—
DINOPHYCEAE																																																						
Ceratium massilinse	—	—	—	—	—	—	—	6.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ceratium sp	—	—	—	1.5	—	—	—	—	—	—	—	—	—	—	—	2.0	0.95	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dinophysis tripos	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Exuviaella sp	—	—	—	6.1	—	—	—	—	7.6	—	—	—	—	—	—	2.0	1.90	—	—	—	1.6	—	—	6.2	8.3	—	—	3.4	11.7	—	8.4	5.7	—	0.9	—	—	—	—	—	—	0.86	—	—	—	—	—	—	—	0.96	—	—	—	—	—
Goniauluax sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.95	—	—	—	—	—	—	6.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gymnodinium sp	—	—	—	—	—	—	—	—	—	—	30.7	8.3	—	0.16	4.7	—	—	9.0	—	4.0	1.0	—	—	—	—	—	21.5	—	11.0	—	—	—	—	—	—	—	—	—	7.6	2.5	—	—	—	—	—	5.8	—	—	—	3.0	2.8	—	—	—
Gyrodinium sp	0.11	—	2.0	—	—	—	6.6	—	—	20.0	—	—	3.3	—	—	6.0	12.3	4.5	1.5	—	1.6	—	11.6	—	8.3	—	5.2	—	5.8	—	—	—	7.6	—	—	—	—	—	—	—	—	—	—	—	—	2.9	5.8	—	—	—	—	—	—	—
Peridinium tuba ?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Peridinium sp	0.11	1.0	—	—	—	—	—	—	—	—	26.9	—	—	0.48	4.7	2.0	—	—	—	8.84	—	—	6.9	—	—	—	15.7	—	—	6.0	0.94	—	—	—	—	—	—	—	3.8	2.5	1.7	—	—	—	—	2.9	—	—	—	4.5	—	5.8	—	—
Peridiniopsis sp	—	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pronoctiluca acuta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prorocentrum micans	0.45	2.5	—	4.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prorocentrum triestinum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Prorocentrum sp	—	—	—	—	14.2	—	—	—	—	—	—	—	—	0.16	—	—	—	—	—	—	—	—	—	—	—	—	5.2	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—	—	—	—	—	4.4	—	—	—	—	—	—	—	—
Pyrophacus sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Warnowia sp	—	—	—	—	—	—	—	—	—	—	—	8.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
CYANOPHYCEAE																																																						
Phormidium sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—	—	—	—	5.8	—	—	—	—	—	0.56	—	—	—
Spirulina sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.4	—	—	—	—	—	—	—	—
Trichodesmium sp	—	—	—	—	—	—	—	—	—	5.0	—	—	—	—	28.5	—	—	—	16.4	5.4	—	—	—	—	—	—	—	—	—	15.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32.2	—	—	—	—	—	4.49	58.8	—	—
Chroococcales	—	—	—	—	—	—	6.6	12.5	—	10.0	7.6	—	—	0.32	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.8	9.0	—	—	—	—	—	—	—	—	—	3.7	—	—	50.0	6.6	—	—	—	85.0	1.92	—	1.6	—	50.0	60.0
CHLOROPHYCEAE																																																						
Clorogonium sp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Clorofitas filamentosas	—	—	—	—	—	—	—	—	—	—	—	—	—	92.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4.5	75.8	—	—	—
No identificadas	—	—	—	—	—	—	—	—	—	—	—	—	—	0.48	14.2	—	—	—	—	—	—	—	—	—	—	—	5.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SILICOFLAGELLATAE																																																						
Dictyocha fibula	—	—	—	—	—	—	—	—	—	—	—	—	—	0.16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dictyocha sp	—	—	2.0	1.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.1	—	—	2.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
FITOFLAGELADAS																																																						
No identificadas	90.9	17.0	10.0	16.9	—	12.5	40.0	37.5	30.7	10.0	26.9	8.3	3.3	0.48	4.7	34.0	2.8	—	—	11.5	—	4.6	6.9	18.7	41.6	0.59	21.5	—	35.2	6.0	—	88.5	23.0	2.7	—	—	1.0	—	21.1	11.2	2.5	—	25.0	13.3	—	4.4	5.8	—	1.9	3.0	3.9	—	—	—
ADDENDUM																																																						
Actinoptychus heptactis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cyclotella striata	—	—	—	—	—	—	6.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dinoflageladas desnudas	—	—	—	—	—	—	13.3	—	—	—	—	16.6	6.6	—	4.7	—	3.8	—	2.2	—	—	—	—	25.0	—	—	—	—	—	—	—	5.7	—	—	—	—	0.6	3.1	—	—	0.8	—	25.0	—	5.8	—	—	—	—	1.5	—	17.6	—	—
Dinoflageladas tecadas	—	—	4.0	—	—	—	—	3.2	7.6	15.0	—	25.0	10.0	—	—	—	0.9	13.6	3.1	—	0.5	—	6.9	25.0	16.6	0.5	15.7	2.3	—	18.1	—	—	—	—	—	—	—	—	3.8	8.7	—	—	—	6.6	2.9	7.3	—	—	—	1.5	0.5	—	—	—
Glenodinium sp	—	—	—	—	—	—	—	—	—	—	—	8.3	—	—	4.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Melosira sulcata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10.0	—	—	—	—	—	—
Thalassiothrix spp	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.2	—	—	—	—	2.9	4.4	—	5.0	—	—	—	—	—	—
DENSIDAD DE FITOPLANCTON																																																						
Células/litro x 1,000	880	200	10	13	1.4	3.2	3	6.4	5.2	4	6.5	2.4	6	153.7	4.2	10	21	4.4	75.2	29.4	74.8	130	8.6	3.2	3	168	2.3	17.2	3.4	4.1	42.4	17.5	4.3	44.4	34	3.20	292	6.4	6.5	8	46.4	0	0.8	3	4.2	8.5	3.4	4	34.6	26.4	22.2	4.2	0.8	1

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[1] La abundancia relativa está referida en porcientos

[2] La densidad se expresa en células/litro

TABLA IV

Composición, abundancia relativa[1] y densidad[2] del fitoplancton de la Bahía de Campeche en invierno (28 enero al 2 febrero 1972)

Estación.	1	7		11			17	26				29		31				36		38	43		50			54		64	66		68		70	76	78	80		84				90				92			
Profundidad metros.	5	5	10	5	10	20	5	5	10	20	40	10	60	5	10	40	80	5	10	5	5	20	5	10	20	5	10	5	5	10	5	10	5	10	5	5	20	5	20	40	80	5	20	40	80	5	20	40	80
BACILLARIOPHYCEAE																																																	
Centricae																																																	
Bacteriastrum delicatulum	–	–	–	–	–	4.6	–	–	–	–	–	–	–	–	–	–	–	–	8.4	–	–	–	–	2.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bacteriastrum elongatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bacteriastrum hyalinum	–	–	–	3.3	–	0.9	–	–	–	–	–	–	–	–	–	–	–	8.5	–	–	–	–	–	2.0	–	1.9	0.7	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bacteriastrum sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Biddulphia sinensis	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cerataulina pelagica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8	–	–	–	–	–	–	–	–	–	–
Chaetoceros coarctatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros compresus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros curvicetus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1	–	–	–	–	9.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11.1	–	–	–	–	–	–	–
Chaetoceros debile	–	–	–	15.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros decipiens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros diversus	–	–	–	–	–	–	10.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros didymus	–	–	–	–	–	–	–	–	–	11.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros laevis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.7	–	–	–	–	–	–	–	–	–	–
Chaetoceros lorenzianus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	12.5	–	–	–	–	–	–
Chaetoceros pendulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Chaetoceros spp	1.0	1.0	–	55.9	–	25.2	12.7	17.2	–	–	9.2	–	–	–	–	–	–	17.0	23.9	–	42.5	17.9	16.6	–	6.4	3.8	6.9	1.3	–	–	0.3	0.5	–	15.5	0.3	7.1	–	50.0	1.4	–	14.2	3.8	–	3.2	–	–	–	9.0	–
Cocconeis sp	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3	0.8	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corethron criophylum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.5	–	–	–	–	–	–	3.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corethron sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.5	–	–	–	0.2	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coscinodiscus radiatus	0.6	0.6	–	–	–	2.8	–	–	–	–	–	8.6	–	2.2	–	6.2	–	–	4.2	–	–	–	–	–	–	–	1.5	–	–	–	0.08	2.6	–	–	0.1	3.5	–	10.0	–	16.6	–	–	2.5	–	–	–	1.1	–	–
Coscinodiscus spp	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	1.3	–	–	–	–	2.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyclotella striata	–	–	–	1.6	–	–	1.1	20.6	–	11.1	0.5	–	–	–	–	–	10.0	–	–	–	–	–	–	–	–	0.6	–	–	3.4	5.8	–	0.8	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	–	–
Cyclotella sp	–	0.3	0.5	–	–	–	–	–	2.3	–	–	8.6	14.8	–	8.3	6.2	6.6	–	–	–	–	–	–	–	0.9	–	0.7	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	–
Eucampia zodiacus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eucampia sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08	2.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Guinardia flaccida	–	–	–	–	–	–	3.4	–	–	–	–	–	–	–	–	–	–	–	1.4	–	–	10.2	–	–	–	1.2	–	–	2.7	–	–	–	–	2.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hemiaulus	–	–	–	–	–	–	–	–	–	4.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leptocylindrus danicus	–	–	–	–	–	–	5.8	10.3	–	–	3.2	–	–	–	–	–	–	3.5	4.2	–	–	5.1	–	–	–	6.4	13.1	–	–	–	12.7	41.7	–	28.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Melosira sulcata	–	2.0	–	–	–	–	–	–	–	–	27.3	–	–	–	–	–	–	–	–	–	–	–	–	8.1	–	–	0.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	50.0	4.0	–	–	41.6
Melosira sp	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia acuminata	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia alata	–	–	–	–	–	–	–	–	–	2.3	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	–	–	23.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia alata f. gracillima	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia alata f. indica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.1	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia bergoni	–	–	–	–	–	–	–	6.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia calcar-avis	–	–	–	–	–	–	–	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	2.5	–	–	2.7	–	–	–	1.3	0.7	0.1	0.2	–	–	–	–	–	–	–	–	–	–	2.5	–	–	–	–	–	–
Rhizosolenia delicatula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia fragilissima	–	–	–	–	6.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.3	3.8	3.1	–	17.1	10.9	2.9	6.5	–	4.4	45.8	–	–	–	–	–	–	–	–	–	–	–	2.3	–	–
Rhizosolenia hebetata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia imbricata v. shrubsolei	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia robusta	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia stolterfothii	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	10.6	5.1	–	–	–	–	1.5	–	10.9	13.8	3.5	16.4	–	11.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhizosolenia spp	–	–	–	–	–	–	–	3.4	–	–	2.7	–	–	–	–	–	–	2.1	–	–	2.1	–	3.5	–	0.9	–	–	–	6.1	–	–	–	–	7.1	–	–	–	–	–	–	–	0.3	–	6.4	–	–	–	–	–
Thalassiosira sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.2	–	–	–	–	–	5.0	–	–	–	–	–	–
No identificada	–	–	1.0	–	–	–	1.1	–	–	–	–	–	3.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.2	–	–	–	–	–	–	12.0	–	–	–
Pennatae																																																	
Amphiprora alata	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphora spp	–	–	1.0	1.6	–	7.4	–	–	–	–	–	–	3.7	–	–	–	–	2.1	1.4	–	–	–	1.1	8.1	7.3	5.7	6.2	–	–	–	0.08	0.5	0.6	1.1	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bacillaria paradoxa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diploneis bombus	–	1.0	1.0	–	–	2.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3	–	0.1	–	–	–	–	–	–	–	–	–	25.0	–	–	–	–
Diploneis weisflogii	0.6	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–	0.7	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Diploneis sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.0	–	–	–	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Grammatophora marina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gyrosigma spenceri	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gyrosigma balticum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gyrosigma spp	–	–	1.0	–	–	3.7	–	–	–	–	1.6	–	–	–	–	–	3.3	–	1.4	–	–	–	–	2.0	–	–	0.7	–	–	–	–	–	0.3	0.5	–	–	–	–	–	–	28.5	–	–	–	25.0	–	–	–	4.1
Mastogloia spp	–	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	10.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	–	–	–	–	–	–	–	–	–	–	–	–	–
Navicula wawrikae	–	–	–	–	–	–	–	–	–	–	–	8.6	–	–	–	–	–	–	–	–	4.2	5.1	–	–	–	–	–	–	–	–	–	1.1	–	0.2	–	–	–	–	1.4	–	–	–	2.5	–	–	–	–	–	–
Navicula spp	4.3	1.3	–	3.3	–	4.6	2.3	–	4.7	–	2.1	–	3.7	–	–	12.5	–	5.6	–	99.7	–	2.5	–	12.2	16.5	–	1.5	–	–	1.4	0.2	–	1.0	0.8	0.9	10.7	–	–	1.4	–	–	–	–	4.3	–	12.0	–	–	–
Nitzschia closterium	0.4	2.3	3.6	5.0	–	8.4	4.6	–	–	–	1.6	–	–	–	–	6.2	–	0.7	–	0.2	–	2.5	5.9	4.0	4.5	7.6	10.8	–	44.5	51.0	4.8	13.7	0.3	5.6	3.7	3.5	–	–	–	–	–	0.3	–	3.2	–	–	–	–	4.1
Nitzschia delicatissima?	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia pacifica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia panduriformis	1.7	–	0.5	–	–	1.8	–	–	–	–	1.0	–	–	–	–	–	–	–	–	–	–	2.5	–	–	–	–	0.7	–	–	–	–	–	0.3	0.5	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia pungens v. atlantica	–	–	–	–	–	2.8	22.0	6.8	–	–	40.9	–	–	–	–	–	–	–	–	–	8.5	10.2	22.6	–	4.5	–	–	–	–	5.8	0.7	–	–	5.3	–	17.8	–	–	–	–	–	74.6	–	18.4	–	–	–	–	–
Nitzschia punctata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	4.3	–	–	–	–	–
Nitzschia sigmoidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nitzschia spp	–	0.6	–	1.6	5.0	3.7	4.6	6.8	–	–	–	4.3	14.8	–	–	–	–	2.8	2.8	–	4.2	–	–	–	6.4	0.6	–	–	2.7	–	0.08	–	1.0	–	–	7.1	–	10.0	4.3	–	–	0.6	–	10.8	–	8.0	–	–	4.1
Plagiogramma vanherckii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Plagiogramma spp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleurosigma normanii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleurosigma spp	1.9	0.3	–	–	–	–	–	–	–	–	2.1	–	–	–	–	–	3.3	–	–	–	–	–	11.9	–	1.8	–	–	–	1.3	2.1	–	5.6	1.0	–	1.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thalassionema nitzschioides	79.5	85.6	86.8	–	–	2.8	29.0	–	–	–	1.6	4.3	7.40	4.5	16.6	–	–	6.3	–	–	4.2	2.5	–	2.0	16.5	8.9	19.3	–	–	–	–	0.5	3.1	0.8	6.6	7.1	4.4	–	2.8	–	28.5	0.3	–	2.1	–	20.0	2.3	18.0	8.3
Thalassiothrix frauenfeldii	0.8	–	–	–	–	1.8	–	13.7	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	2.3	10.2	–	3.8	–	–	–	–	–	–	1.0	–	–	–	8.8	10.0	2.8	–	–	0.3	–	6.5	–	–	–	9.0	–
No identificadas	–	1.7	1.5	1.6	–	0.9	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	4.0	1.8	1.9	–	–	4.1	5.1	–	0.5	–	3.2	–	–	–	–	1.4	–	–	–	–	–	–	–	1.1	9.0	–
DINOFLAGELLATAE																																																	
Amphidinium carteri	0.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphidinium spp	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	–	0.9	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ceratium furca	–	–	–	1.6	–	–	–	–	–	11.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ceratium fusus	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	10.0	–	–	–	–	–	–	–	–	–	–	–
Coclodinium sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dissodinium lunula	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Exuviaella sp	1.5	–	–	–	–	3.7	–	–	–	–	–	–	–	–	–	–	–	0.7	–	–	–	5.1	–	–	–	4.4	–	2.7	–	0.7	–	–	–	1.4	–	–	–	–	–	–	–	0.3	–	–	–	–	–	–	–
Goniaulax spp	0.2	–	–	–	–	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.5	–	–	0.9	3.8	2.3	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	8.0	–	–	–
Gymnodiniales spp	–	1.0	–	–	–	5.6	–	–	4.7	–	–	–	–	–	–	–	–	2.8	1.4	–	2.1	–	–	–	–	–	1.5	–	–	0.7	2.8	0.5	1.7	–	35.8	–	–	–	5.7	66.6	–	3.8	–	–	–	8.0	–	–	–
Gymnodinium sp	–	–	–	–	1.6	–	–	–	9.52	11.1	–	4.3	3.7	18.1	–	12.5	10.0	–	–	–	2.1	–	–	10.2	–	–	–	–	–	–	–	–	–	–	–	–	2.2	–	8.6	–	–	–	5.0	–	–	–	11.9	–	29.1
Gyrodinium spp	–	–	–	–	–	–	–	3.4	–	–	–	–	–	–	–	–	–	–	–	–	6.3	–	5.9	–	1.8	1.9	3.1	–	–	–	–	–	–	–	0.2	–	–	–	–	16.6	–	0.3	–	–	–	–	–	–	–
Peridiniales spp	0.8	–	–	–	–	5.6	–	–	14.2	–	–	8.6	3.7	4.5	25.0	–	–	2.8	1.4	–	–	–	–	–	–	5.1	–	1.3	–	–	–	–	–	0.8	–	3.5	–	–	–	–	–	–	–	–	–	–	–	–	–
Peridinium splendens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	–	–
Peridinium spp	–	–	–	–	1.6	–	–	–	–	–	–	8.6	3.9	6.8	–	–	13.3	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	8.8	–	2.8	–	–	–	7.5	–	–	–	5.9	–	–
Podolampas spinifer	–	–	–	–	–	–	–	–	–	11.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Prorocentrum gracile	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Prorocentrum micans	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.3	–	–	–	–	4.1	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	–	–	–	–	–	–
Prorocentrum scutellum	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Prorocentrum triestinum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Prorocentrum spp	–	0.3	–	–	–	–	–	–	–	22.2	–	4.3	–	6.8	–	–	3.3	–	–	–	–	5.1	–	–	–	–	0.7	–	2.7	–	–	–	–	–	–	–	–	–	1.4	–	–	–	–	–	–	–	2.3	–	–
CYANOPHYCEAE																																																	
Chroococcaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	4.5	–	–	–	–	11.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spirulina sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–	–	–
Phormidium sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trichodesmium spp	–	–	1.0	–	83.3	–	–	–	–	–	–	–	25.9	–	–	–	–	9.9	4.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–	32.6	–	–	–	–	–
CHLOROPHYCEAE																																																	
Chlorella sp	–	–	–	–	–	–	–	–	19.0	–	–	17.3	14.8	11.3	25.0	25.0	6.6	–	–	–	–	–	–	4.0	–	–	–	–	–	–	–	–	–	–	–	–	51.1	–	30.4	–	–	–	45.0	–	–	–	20.2	–	8.3
Clorofitus filamentosos	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.0	–	–	–	–	–	–	–	–	–	–	–	–	60.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SILICOFLAGELLATAE																																																	
Dictyocha fibula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.0	–	–	–	–	–	–	–	0.8	–	–	–	3.5	–	–	1.4	–	–	–	–	–	–	–	–	–	–
Dictyocha spp	4.30	0.3	–	–	–	0.9	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	2.1	–	–	–	0.9	16.0	20.1	–	–	–	0.08	–	–	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–
FLAGELLATAE																																																	
Fitoflageladas no identificadas	0.6	0.6	1.5	1.6	–	2.8	1.1	10.3	33.3	22.2	2.7	21.7	–	36.3	16.6	31.2	30.0	1.4	1.4	–	4.2	–	15.4	–	13.7	20.5	0.5	61.6	2.0	1.4	0.8	1.1	–	0.5	0.3	32.7	15.5	10.0	10.1	–	14.2	2.2	7.5	2.1	–	28.0	47.6	54.5	–
ADDENDA																																																	
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–	–	–
Actinoptychus heptaclis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–	–	–
Cianofitas Chroococcales	–	–	–	–	–	–	–	–	–	–	–	–	–	4.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.5	–	–	–	–	–	–
Cianofitas Hormogonales	–	–	–	–	–	–	–	–	4.7	–	–	–	–	–	8.3	–	–	–	–	–	–	–	–	2.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.2	–	–	–	2.5	–	–	–	–	–	–
Eucampia cornuta	–	–	–	–	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gyrosigma balticum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hemiaulus membranaceus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pyrophacus sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14.2	–	–	–	–	–	–	–	–
Rhizosolenia setigera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.9	7.0	–	–	–	–	–	–	–	–	–	–	–	–	–	83.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Skeletonema costatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.4	–	–	–	–	–
Thalassiosira sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trichodesmium sp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
DENSIDAD DE FITOPLANCTON																																																	
Células/litro x 1,000	465	292	190	11.8	7.5	21.2	28.6	5.8	5.2	1.5	37.2	3.8	4.5	5.5	2	2	3.7	28.2	23.6	1705	9.4	7.8	33.7	8.1	43.6	156	129	14.6	146	137	1133	335	287	334	753	5.6	5.6	2	8.6	1.2	1.4	126	5	36.8	0.8	5	14	2.2	5

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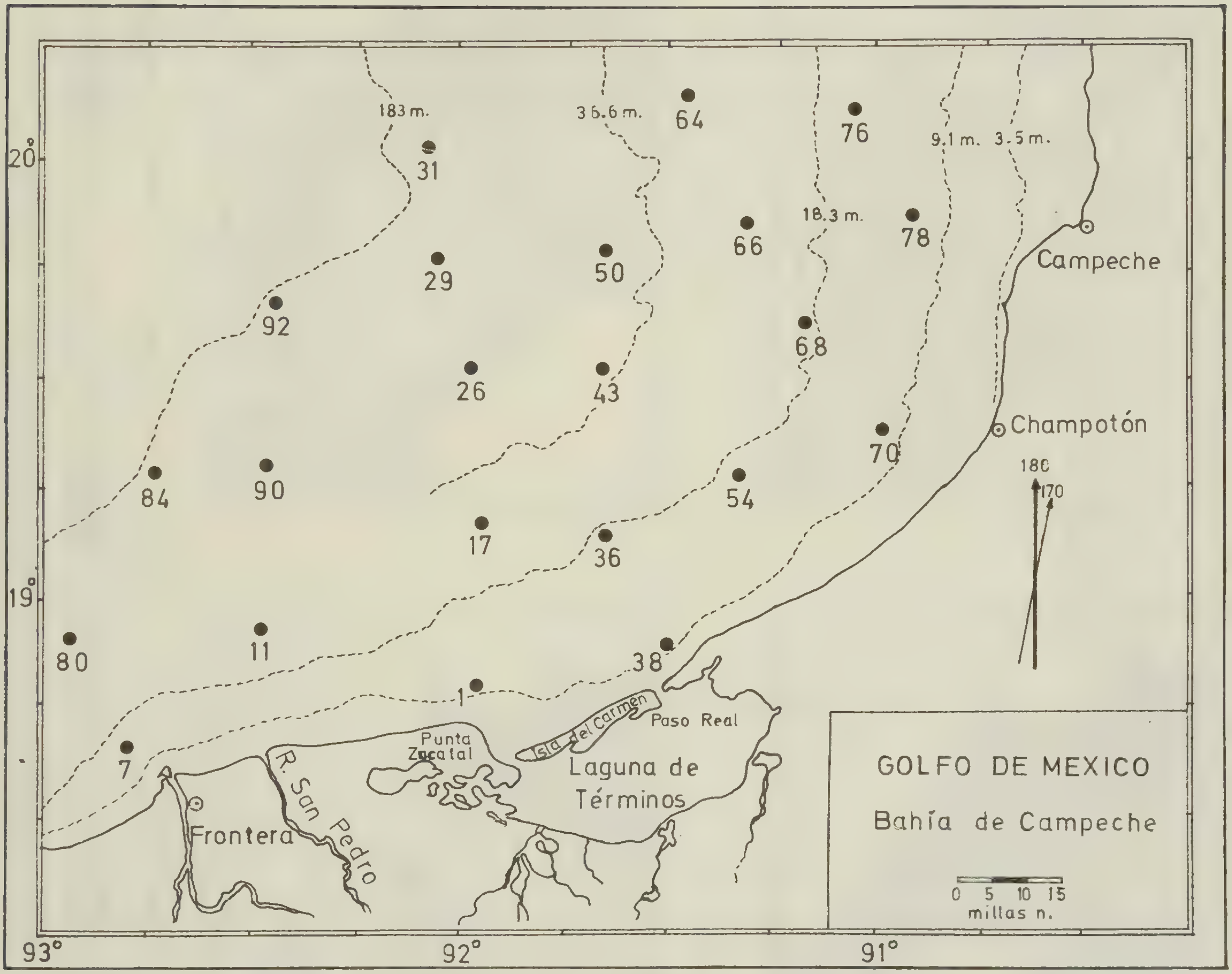
[1] La abundancia relativa está referida en porcientos

[2] La densidad se expresa en células/litro


183 m.
36.6 m.
18.3 m.
9.1 m.
3.5 m.
20°
19°
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66
78
29
50
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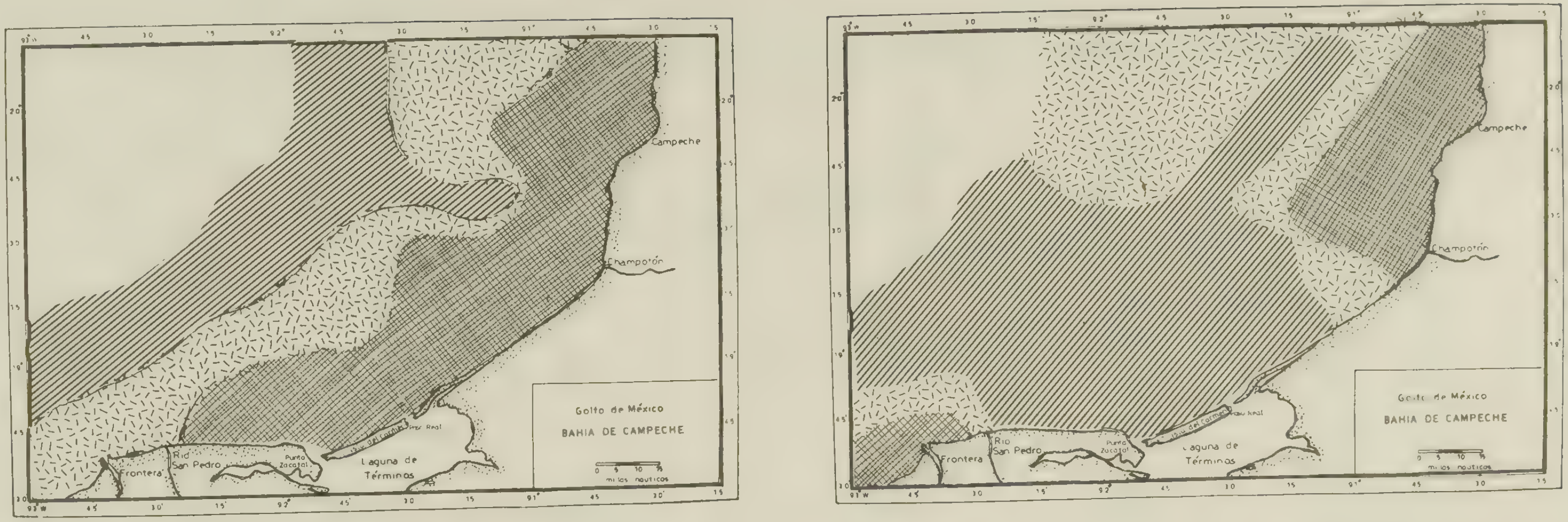
68
26
43
70
84
90
54
17
36
80
11
38
1
7
Campeche
Champotón
180
170
Punta Zacatal
Isla del Carmen
Paso Real
Laguna de Términos
Frontera
R. San Pedro
GOLFO DE MEXICO
Bahía de Campeche
0 5 10 15
millas n.

Fig. 1 Area de Estudio


Campeche
Champotón
Golfo de México
BAHIA DE CAMPECHE
Laguna de Términos
Isla del Carmen
Paso Real
Punta Zacatal
Rio San Pedro
Frontera
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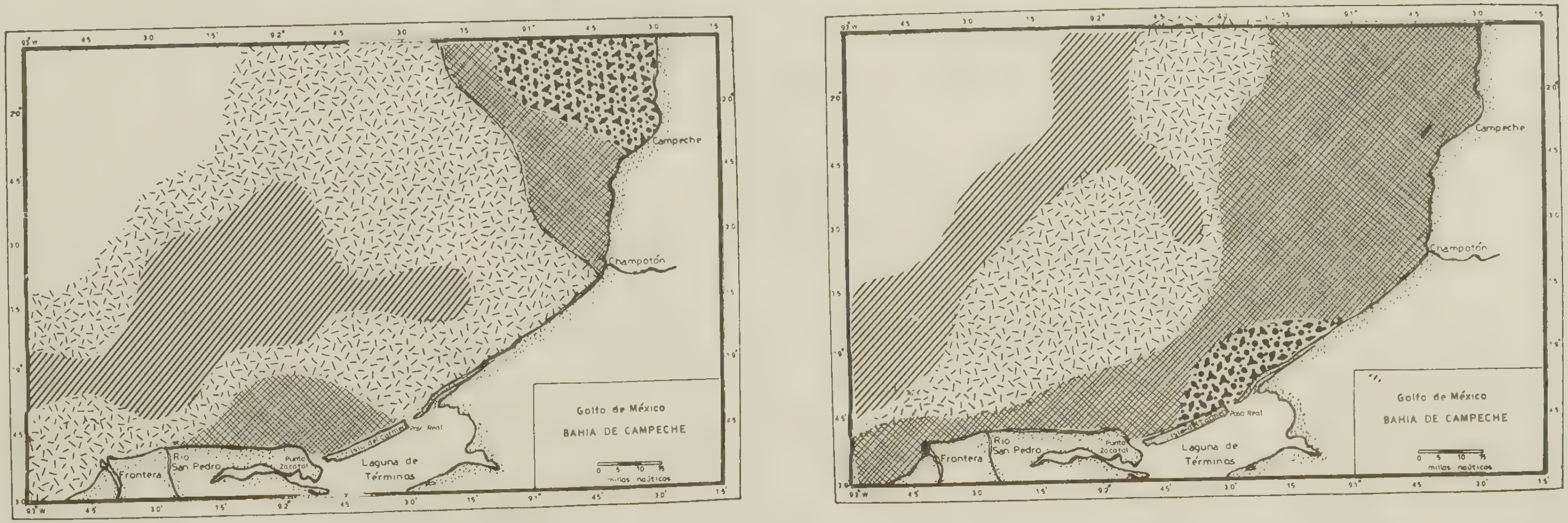
Campeche
Champotón
Golfo de México
BAHIA DE CAMPECHE
Laguna de Términos
Isla del Carmen
Paso Real
Punta Zacatal
Rio San Pedro
Frontera
millas naúticas

OTOÑO 21-26 sep. 1971

INVIERNO 28 ene.-2 feb. 1972

▨ $<$de 10^4 céls./l.   ░ de 10^4 a $<10^5$ céls./l.   ▩ de 10^5 a $<10^6$ céls./l.   ▦ de 10^6 a $<10^7$ céls./l.

Fig. 2 Variación estacional de la densidad promedio del fitoplancton en la Bahía de Campeche. Se muestran las zonas de concentración de organismos

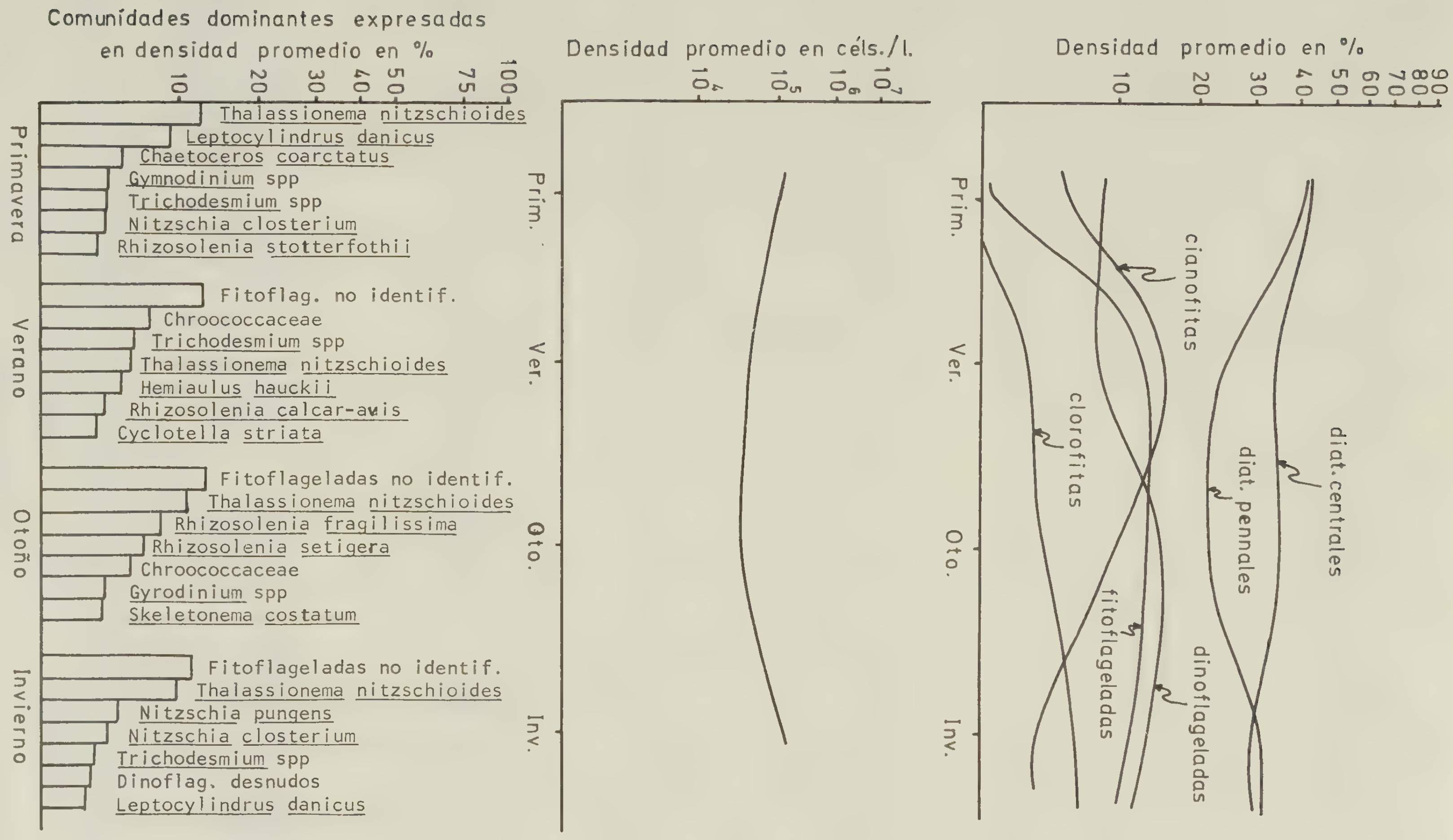

Fig. 3

A

Variación estacional de la densidad promedio relativa (en %) de los grupos mayores que componen el fitoplancton

B

Variación estacional de la densidad promedio del fitoplancton de todos los grupos, expresada en cél/l

C

Variación estacional de las comunidades dominantes referidas en densidades promedio porcentuales

Este período se caracterizó por densidades bajas, ya que la mayor parte de la bahía registró cifras inferiores a 10^4 cél/l y sólo una pequena zona costera frente a los ríos Frontera y Champotón tuvieron valores promedio que oscilaron entre 350 000 y 620 000 cél/l. La región norte de la bahía se caracterizó por presentar cifras entre 10 000 y 17 000 cél/l (Fig. 2). La densidad de células promedio fue de 56 150 cél/l.

4.3 Otoño

En esta época se registró mayor abundancia de las dinoflageladas en relación a los otros períodos, registrando una densidad promedio de 15,2 por ciento; las fitoflageladas mantuvieron en promedio la misma densidad que se observó en el verano, y las cianofitas empezaron a descender en su abundancia (9,1 por ciento). Las diatomeas tanto centrales como pennales tuvieron proporciones similares a las del verano. Las clorofitas manifestaron un leve ascenso con respecto al verano (Fig. 3A).

Esta temporada registró el valor promedio en densidad más bajo a través del ciclo anual y fue del orden de 45 770 cél/l, que en realidad no difiere en mucho de los valores que se registraron en verano.

La zona de mayor densidad alcanzó un valor de 3,2 millones de cél/l, pero limitada a la costa frente a Campeche, siendo la causa una floración de *Rhizosolenia fragilissima*, cuya población dominó en un 99,93 por ciento. Por el lado opuesto la mayor parte del área registró cifras que oscilaron entre 10^4 y $<$ de 10^5 cél/l. Parte de la región central y occidental presentó cifras inferiores a 10^4 cél/l y sólo frente a la boca de Punta Zacatal de la Laguna de Términos se registró un valor promedio de 540 000 cél/l (Fig. 2).

4.4 Invierno

En este tiempo las cianofitas registraron la densidad promedio más baja en el año, con un valor de 3,5 por ciento y las algas verdes el valor más alto con 6,9 por ciento. Las flageladas en general no manifestaron cambio en relación a la época anterior. Las diatomeas continuaron siendo dominantes (Fig. 3A).

La zona de mayor densidad se localizó frente a la boca de Paso Real de la Laguna de Términos con un valor de 1,7 millones de cél/l producto de una floración de *Navicula* que no fue posible determinar, y que constituyó la población dominante en un 99,7 por ciento. El patrón de las isoplanctas muestra un claro gradiente de la costa hacia el norte de la bahía, muy similar a lo encontrado en la época primaveral, pero con una densidad promedio mayor (134 500 cél/l) y que fue la mayor registrada en el ciclo anual estudiado.

5. DISTRIBUCION DE LAS COMUNIDADES MAS IMPORTANTES

5.1 Primavera

En este tiempo destacaron: *Chaetoceros* spp., distribuido ampliamente en toda el área, particularmente como población dominante en varias estaciones frente a la Laguna de Términos, y como subdominante frente a Campeche y Champotón; *Thalassionema nitzszchioides*, se localizó en toda el área, pero con mayor abundancia en los sitios cercanos a la costa. *Rhizosolenia stolterfothii* destacó por su abundancia en la región central de la bahía; diversas especies de los géneros *Coscinodiscus*, *Amphora*, *Navicula*, *Nitzschia*, *Thalassiothrix* y diatomeas pennales no identificadas, se localizaron distribuidas en toda el área, sin embargo, no constituyeron poblaciones numéricamente importantes. *Leptocylindrus danicus* con escasa distribución, se encontró como población dominante en las estaciones 76 y 78 con altos porcentajes en abundancia relativa (Tabla I).

Las cianofitas representadas por el género *Trichodesmium* se ubicaron en sitios restringidos, distinguiéndose por su abundancia en algunas estaciones del área central. Las dinoflageladas desnudas se encontraron con amplia distribución, aunque con mayor abundancia en la región norte del área; las silicoflageladas y cocolitofóridas cuya presencia se puede considerar excepcional, se registraron únicamente en las estaciones 17 y 11 respectivamente.

5.2 Verano

En esta época destacaron: *Skeletonema costatum*, que estuvo bien representada en el área frente al Río Frontera, en donde se registró la mayor densidad fitoplanctónica, y con menores por cientos de abundancia en las estaciones 80 y 92; *Chaetoceros coarctatus* aunque fue abundante en superficie formando el 73 por ciento de la comunidad dominante, quedó limitado a la estación 36. *Thalassionema nitzschioides* se localizó en la mayor parte del área, pero con mayor abundancia en la región oriental de la bahía; *Nitzschia closterium* destacó frente a la Laguna de Términos, siendo escasa en las áreas más alejadas a la costa. *Cyclotella striata* fue dominante en las muestras de fondo especialmente en la estación 84; *Hemiaulus hauckii* manifestó su mayor densidad en las muestras de fondo particularmente en la costa nordeste. *Rhizosolenia calcar-avis* se desarrolló mejor en la región nordeste (Tabla II).

Varias especies de fitoflageladas no identificadas se encontraron ampliamente distribuidas en el área, destacando numéricamente en las estaciones de la región occidental. Entre las cianofitas dominó el género *Trichodesmium*, localizado más bien en los sitios alejados de la costa; otras cianofitas no identificadas se localizaron en el área de influencia del Río San Pedro.

5.3 Otoño

Las fitoflageladas se localizaron en toda el área, pero con mayor abundancia en los sitios cercanos a la costa constituyendo poblaciones dominantes, especialmente en las estaciones cercanas a la Laguna de Términos. *Chaetoceros* spp. se encontraron bien representados en la mayor parte de la bahía. *Thalassionema* sp. especialmente *T. nitzschioides* se encontraron distribuidas en toda el área, llegando a ser dominantes en las regiones límites oriental y occidental de la bahía. El género *Rhizosolenia* estuvo representado por varias especies con amplia distribución, destacando por su abundancia *Rh. fragilissima*, que se ubicó en la región central como población dominante (Tabla III).

Entre las dinoflageladas sobresalieron: *Exuviaella* spp., *Peridinium* spp. y *Gymnodinium* spp. con una amplia distribución en el áraa. Las silicoflageladas representadas por el género *Dictyocha* se detectaron en forma escasa en la región norte de la bahía.

5.4 Invierno

En esta época destacaron por abundancia el género *Rhizosolenia*, que se localizó en las estaciones situadas al frente entre Champotón y Campeche, destacando *R. stolterfothii*, *R. alata*, *F. gracillima* y *R. setigera*, algunas de estas especies se encontraron asociadas constituyendo poblaciones dominantes en algunas localidades. Los *Chaetoceros* spp. se localizaron como dominantes en las estaciones situadas frenta a Boca de Paso Real y como subdominantes frente a la Punta Zacatal de la Laguna de Términos; el género *Navicula* con amplia distribución en el área se presentó como dominante en un 99 por ciento frente a la Boca de Paso Real. *Thalassionema nitzschioides* se registró en la mayor parte de la bahía, pero con mayor abundancia frente al Río Frontera y la Punta Zacatal. *Nitzschia closterium* se localizó con mejor desarrollo en la región oriental de la bahía. *Leptocylindrus danicus* se encontró como población dominante en la estación 76 y como subdominante en las estaciones de la región central del área. Algunas especies de *Coscinodiscus*, *Thalassiothrix frauenfeldii*, dinoflageladas desnudas y fitoflageladas no identificadas se localizaron ampliamente distribuidas pero no llegaron a constituir poblaciones dominantes (Tabla IV).

De las cianofitas sobresalió por su abundancia el género *Trichodesmium*, desarrollándose mejor frente al área de la desembocadura del Río San Pedro. Las clorofitas estuvieron representadas en mayor porcentaje por *Chlorella* sp., siendo más abundantes en la región occidental de la bahía.

6. DISCUSION Y CONCLUSIONES

A juzgar por las cifras promedio de los análisis cuantitativos, se puede decir que la Bahía de Campeche registra una alta producción de fitoplancton en el invierno (134 500 cél/l), la cual empieza a disminuir gradualmente hasta en un tercio de su capacidad hacia el otoño (45 770 cél/l). Sin embargo, a través del año se registran florecimientos de diatomeas y fitoflageladas que indudablemente tienen importancia local.

De acuerdo a las variaciones cualitativas y cuantitativas se pueden identificar tres zonas ecológicas:

(a) La zona costera con alta densidad fitoplanctónica oscilando entre 10^5 y <de 10^6 cél/l y compuesta por especies neríticas y salobres;

(b) la región central de la bahía caracterizada por presentar desplazamientos horizontales perpendiculares a la costa y con valores de densidad alrededor de 10^5 cél/l;

(c) la región norte de la bahía con flora de estirpe oceánica y cifras de densidad inferiores a 10^4 cél/l.

Respecto a la temperatura y la aparición de las diferentes especies no se pudo obtener un cuadro claro, debido a que gran parte de las diatomeas que constituyeron el grupo dominante son cosmopolitas euritermas; sin embargo, se notó la influencia de la temperatura en la aparición de los grupos más estenotermos como son las dinoflageladas, cuya mayor abundancia surgió en otoño relacionada con temperaturas altas (entre 28 y 29°C, según Villalobos *et al.*, 1975). Es evidente que debido a la falta de conocimiento de los nutrientes, resulta difícil dilucidar algunos problemas sobre la ecología del fitoplancton, pero si se puede establecer la secuencia general de las poblaciones como se enmarca a continuación:

De las especies que destacaron durante el florecimiento a fines de invierno que se prolongó hasta el inicio de la primavera, se observaron diferencias en las poblaciones en estos dos períodos, pero manteniendo el pulso de proliferación; así, en invierno, dominaron por orden de abundancia el género *Navicula* que se desarrolló como población absoluta (99 por ciento), frente a la Boca de Paso Real, *Rhizosolenia setigera*, *Thalassionema nitzschioides*, *Nitzschia delicatissima*, *Nitzschia closterium*; fitoflageladas varias especies del género *Chaetoceros*, *Rhizosolenia fragilissima* y *Leptocylindrus danicus*; a la primavera le sucedieron incrementos en las poblaciones de *Leptocylindrus danicus* y *Thalassionema nitzschioides* con la aparición de las especies *Skeletonema costatum*, *Trichodesmium* spp., *Nitzschia delicatissima*, *Chaetoceros coarctatus* y *Rhizosolenia stolterfothii*. En el verano que sufrió un decremento en la densidad fitoplanctónica, se observó que las poblaciones de *Skeletonema costatum* y *Chaetoceros coarctatus* se desarrollaron mejor que en la primavera, pero también destacaron *Hemiaulus hauckii*; algunas cianofitas, *Thalassionema nitzschioides*, *Rhizosolenia calcar-avis*; ciertas flageladas y *Nitzschia closterium*. Finalmente en el otoño en que se ubicó la menor diversidad de especies con un leve florecimiento, destacaron las especies *Thalassionema nitzschioides*; algunas fitoflageladas, *Skeletonema costatum* y *Rhizosolenia setigera*.

Como ha podido observarse, se refleja una clara predominancia de las diatomeas en relación a los demás componentes del fitoplancton. Las dinoflageladas se ubicaron en segundo término, aunque en algunos momentos esto pudiera no ser en la realidad lo cierto, ya que de acuerdo a las observaciones que Hasle (1959) ha hecho en el sentido del tamaño de las muestras en relación a la cuantificación de las dinoflageladas, los volúmenes que aquí se analizaron (25 cm^3) quedan muy por debajo de los volúmenes que se recomienda analizar. A esto hay que agregar la pobreza de nuestra identificación taxonómica, ya que en este sentido muchas de las especies que en las Tablas I a IV aparecen agrupadas bajo el título de fitoflageladas, gran parte pudieron corresponder a dinoflageladas del tipo desnudo.

En relación al alto contenido de oxígeno disuelto que Villalobos y Zamora (*op. cit.*) reportan en invierno hasta de 8 y 10 ml/l no se pueden atribuir a la actividad fotosintética, sino más bien es probable atribuirlos a los procesos físico-químicos o al efecto de los fuertes "nortes" tan característicos en esta época. Relaciones similares pero inversas se encontraron en primavera, es decir bajos valores de oxígeno disuelto con abundancia de fitoplancton; en este sentido Gómez, 1965; Smayda, 1966; Angot, 1968; Santoyo, 1972; y Santoyo y Signoret, 1973, han encontrado relaciones similares.

De acuerdo a la información que se ha obtenido de la Laguna de Términos por los trabajos de Loyo-Rebolledo, 1966; y Gómez Aguirre, 1965, y el presente estudio, se ha encontrado una gran concordancia en la composición general del fitoplancton, especialmente la lista de especies de las estaciones que están ubicadas paralelamente a la costa, por lo que resulta obvio un intercambio de flora planctológica entre la Laguna de Términos y la región costera adyacente. También se ha podido constatar en base a la diferente estirpe y composición de las comunidades fitoplanctónicas, que la Boca del Carmen de la Laguna de Términos tiene mayor influencia estuarina hacia la Bahía de Campeche en comparación con la Boca de Paso Real, por lo que suponemos que por ésta penetra la mayor cantidad de flujo marino que recibe la Laguna de Términos. A este respecto de la Lanza, 1976, estudiando la hidrología de la Bahía de Campeche, ha encontrado que la hidrodinámica de esta área está dada por la influencia de aguas continentales que circulan paralelamente a las costas, dando origen a un movimiento perpendicular a las mismas, contribuyendo a la formación de núcleos turbulentos con sentido ciclónico entre Campeche y Laguna de Términos. Observaciones similares se encuentran en Gutiérrez, 1976, quien afirma que las corrientes de deriva superficiales en el frente deltico y litoral de Yucatán se desplazan hacia el oeste.

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STUDIES OF CARIBBEAN ZOOPLANKTON[1]

by

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1. INTRODUCTION
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Abstract

Plankton and hydrographic data collected at 105 stations during nine cruises in oceanic Caribbean and adjacent waters, including the Florida Straits and Gulf of Mexico, have been analysed for species occurrence, relative abundance, horizontal distribution, and vertical distribution in relation to water masses. Plankton was sampled in horizontal tows of opening-closing 3/4 m nets at several levels between surface and bottom. All species of Siphonophora, Heteropoda, Euphausiacea, Chaetognatha and Salpidae were identified and counted. Because over 400 pelagic copepod species occur in the area, 20 species common in major portions of the water column were individually counted, and the remainder were enumerated as totals of calanoids, harpacticoids and cyclopoids. Cyclopoids almost equal calanoids numerically. Donald Haagensen analysed thecosome molluscs. The Office of Naval Research is sponsoring publication of a report on these seven groups. Other groups being studied are Amphipoda, bathypelagic Copepoda and Ostracoda, and Halobates.

Greatest numbers occurred in Tropical Surface Water and Subtropical Underwater (upper 200 m), but many species are essentially restricted to Subantarctic Intermediate and North Atlantic Deep Water. Temperature-Salinity-Plankton diagrams clearly illustrate vertical distribution of species. Animals were most abundant in the central Caribbean and the Central American bight. Hydrographic and biological data showed upwelling off Venezuela, Colombia, Panama, Costa Rica, and Nicaragua. Although certain copepod and thecosome species are reliable indicators, chaetognaths are the most broadly useful labels of upwelling, coastal and oceanic influence, and perhaps, movement of North Atlantic Central Water into the Caribbean.

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Resumen

En el curso de nueve viajes realizados en el Caribe y aguas adyacentes, incluido el estrecho de la Florida y el Golfo de México, se han recogido plancton y datos hidrográficos en 105 puntos distintos, que se han analizado posteriormente para determinar las especies presentes, su abundancia relativa, su distribución horizontal y su distribución vertical en relación con las masas de agua. Las muestras de plancton se tomaron en lances horizontales de arrastre con redes de abrir y cerrar de 3/4 m, a varias profundidades entre la superficie y el fondo. Se individuaron y contaron todas las especies de Siphonophora, Heteropoda, Euphausiacea, Chaetognatha y Salpidae. Dado que en la zona se encuentran más de 400 especies de copépodos pelágicos, se contaron individualmente 20 especies que se encuentran comúnmente en las zonas principales de la columna de agua y, para el resto, se enumeraron los totales de calanoideos, harpacticoideos y ciclopoideos. El número de ciclopoideos y calanoideos resulta casi idéntico. Donald Haagensen analizó los moluscos tecosomatos. La Oficina de Investigaciones Navales patrocina la publicación de un informe sobre estos siete grupos. Otros grupos estudiados son Anfipoda, Copepoda y Ostracoda batipelágicos, y Halobates.

La mayor abundancia se encontró en aguas superficiales tropicales y aguas subyacentes subtropicales (en los 200 m superiores), pero muchas especies se encuentra solamente en aguas profundas intermedias subantárticas o noratlánticas. Los diagramas de temperatura-salinidad-plancton muestran claramente la distribución vertical de las especies. Donde mayor abundancia se encontró fue en el centro del Caribe y en el seno centroamericano. Los datos hidrográficos y biológicos muestran zonas de afloramiento frente a Venezuela, Colombia, Panamá, Costa Rica y Nicaragua. Aunque algunas especies de copépodos y tecosomatos son indicadores fidedignos, los quetognatos constituyen las señales más claras de la presencia de afloramientos de influencias costeras y oceánicas y, quizás, del desplazamiento de las aguas de la parte central del norte del Atlántico hacia el Caribe.

1/ Contribución de la Rosenstiel School of Marine and Atmospheric Science, Universidad de Miami, Miami, Florida, EE.UU.

1. INTRODUCTION

At the CICAR-I meeting, Owre and Foyo (1971) described a broad study of oceanic zooplankton in the Caribbean in progress under the auspices of the University of Miami. That programme has now been concluded. The U.S. National Science Foundation supported it from September 1966 until September 1968 and from May 1969 to May 1970 (GB-5625 and GB-13113). NSF Grants GB-3808, GB-5776 and GB-7082 funded shipboard operations. Since April, 1971, analysis of data and preparation of reports have been supported by the U.S. Office of Naval Research under Contract N 0014-67-A-0201-0013. We now summarize the scope and results of the study and conclude with a list of references pertinent to research on plankton in the Caribbean area. We have eliminated references to hydrographic studies which are included in reports to agencies, as well as biological references cited in our first CICAR paper. The citations are grouped in the following categories: zooplankton, Siphonophora, Heteropoda, Copepoda, Euphausiacea, Chaetognatha and Salpidae. Another planktonic group was studied by D.A. Haagensen, whose Master's Thesis (University of Miami) and Scientific Report to ONR Project NR-083-060 is titled "Thecosomata (Gastropoda, Opisthobranchiata) of the Caribbean Sea and adjacent areas" (342 pp.). Haagensen reported 29 species and 13 formae. A revision of the thesis forms Part II of Michel, Foyo and Haagensen (1976). Still in progress is a study by Kenneth Kimball, of the Amphipoda Hyperiidea collected at selected stations in the eastern Caribbean and the Atlantic north of Puerto Rico and Hispaniola. Kimball has identified 76 species, of which 40 are new records for the area.

Interim and final reports to the granting agencies are cited in references on zooplankton (Owre and Foyo, 1971; Owre (Michel) and Foyo, 1972; Owre and Low, 1969; Michel, Foyo and Haagensen, 1976) and on Chaetognatha (Owre, 1972, 1973). Since complete documentation can be found in Michel, et al. (1976), no specific references to previous work will be made in the present text.

From June 1966 to November 1969 hydrographic data and plankton samples were collected on eight cruises in oceanic waters of the Caribbean Sea and adjacent areas, including the eastern Gulf of Mexico. Horizontal tows, monitored by Benthos Time-Depth Recorders, were made with mechanically opened and closed nets at several depths between surface and bottom. Throughout the programme conical nets 3.5 m long, 75 cm in diameter at the mouth and 10 cm in diameter at the cod end were used. These were constructed of three grades of nylon netting, the mesh sizes being 100 µm in the cod end section, 1.6 mm in the mid-section and 3.2 mm at the forward end. Each net was sent to the desired depth tightly rolled and secured, opened at depth, fished for one hour and closed by choking before retrieval. The samples were collected in unvarying routine and they are comparable but not quantitative. The use of flow meters was discontinued early in the programme because reliable readings could not be obtained regularly at all depths sampled on station with any type of flow meter available. Hydrographic data were collected immediately before plankton sampling. Stations at which any of the prodedures were not properly completed for any reason were eliminated from consideration. The complete series of samples, with hydrographic data, collected at 105 stations form the basis for our report. The locations of these stations are shown in Fig. 1.

Hydrographic casts, with Niskin bottles and reversing thermometers, were made on the first four cruises (40 stations), yielding data on oxygen and PO_4-P as well as temperature and salinity. A Bissett-Berman STD system (Model No. 9006) was used to record temperature and salinity to a maximum depth of 1 500 m on the last four cruises (65 stations).

Procedures in plankton sampling depended on bottom depth. In water 2 000-2 500 m deep, six nets were put on the wire, the deeper ones spaced to sample 500-1 000 m apart, the shallower ones 250 m apart and the shallowest in the lower Tropical Surface Water or upper Subtropical Underwater near the thermocline, if present. A seventh net, suspended from a boom and independent of the wire, sampled the surface waters as the deeper nets were opened. Thus seven essentially simultaneous one-hour samples were collected. Depths greater than 2 000-2 500 m were sampled in separate three-net casts. For example, at a station with a bottom depth of 4 334 m, the nets of the first cast were set to sample at 0, 60, 250, 500, 1 000, 1 500 and 2 000 m, and those of the second cast, at 2 500, 3 500 and 4 000 m. The

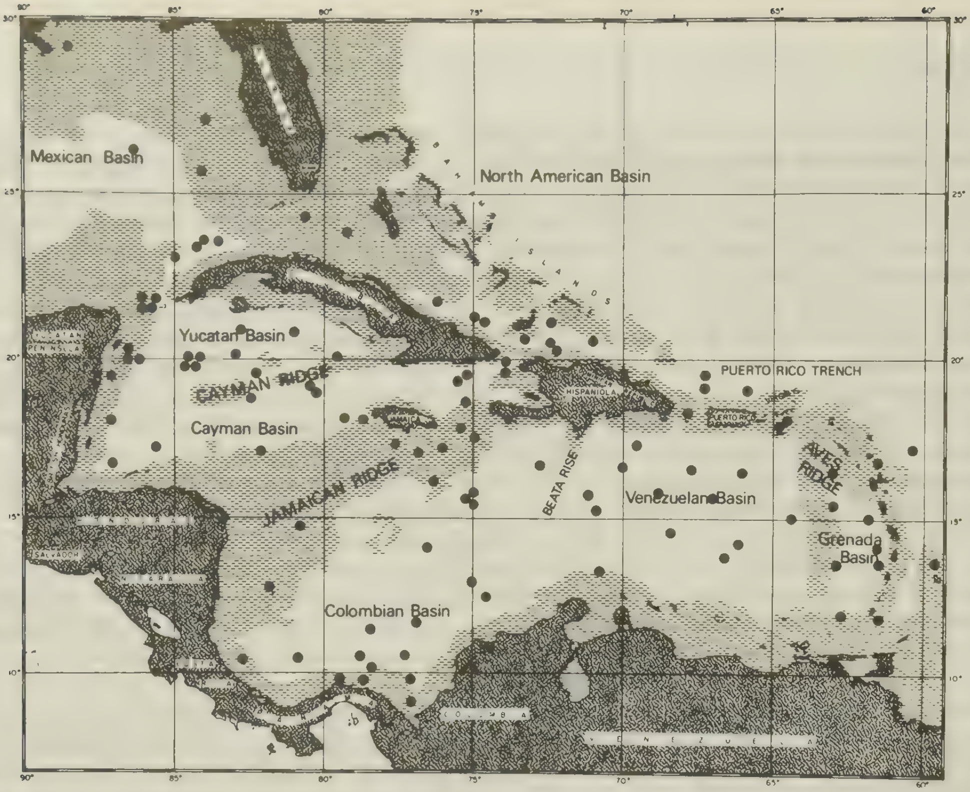
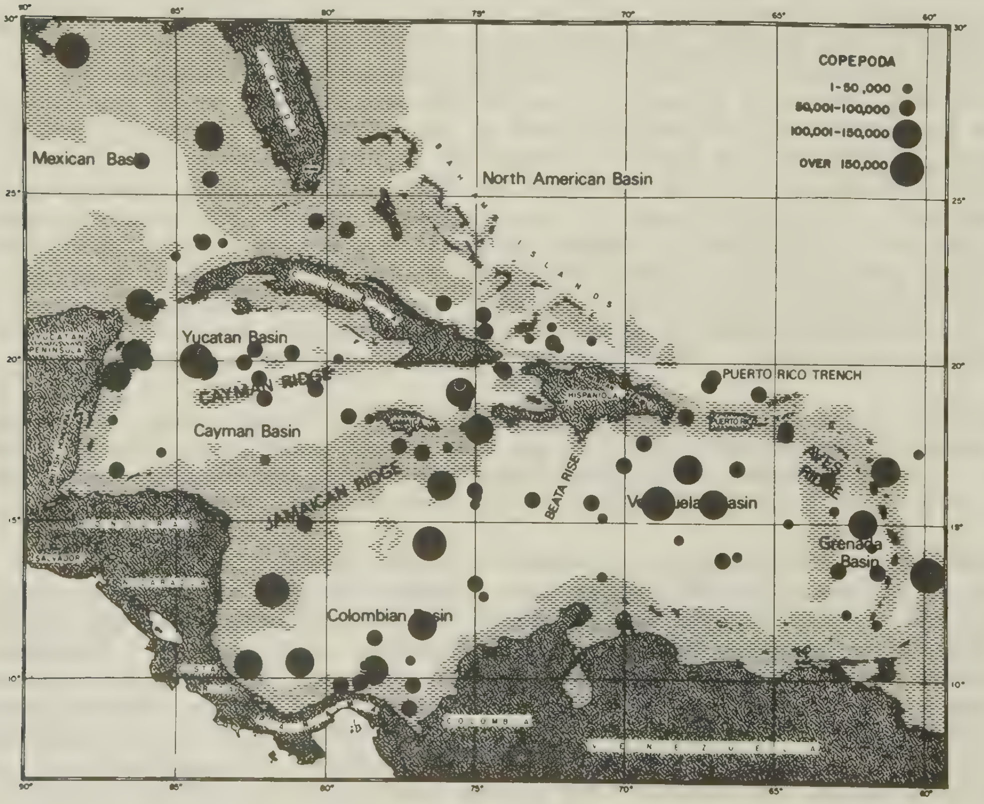

90°
85°
80°
75°
70°
65°
60°
30°
25°
20°
15°
10°
Mexican Basin
North American Basin
BAHAMA ISLANDS
Yucatan Basin
CAYMAN RIDGE
Cayman Basin
JAMAICAN RIDGE
BEATA RISE
Venezuelan Basin
PUERTO RICO TRENCH
HISPANIOLA
AVES RIDGE
Grenada Basin
Colombian Basin
COLOMBIA
VENEZUELA

Fig. 1 Locations of stations at which hydrographic data and complete series of plankton samples were obtained


90°
85°
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60°
30°
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15°
10°
COPEPODA
1-50,000
50,001-100,000
100,001-150,000
OVER 150,000
Mexican Basin
North American Basin
BAHAMA ISLANDS
Yucatan Basin
CAYMAN RIDGE
Cayman Basin
JAMAICAN RIDGE
BEATA RISE
Venezuelan Basin
PUERTO RICO TRENCH
HISPANIOLA
AVES RIDGE
Grenada Basin
Colombian Basin
COLOMBIA
VENEZUELA

Fig. 2 Total numbers of copepods collected at all depths combined at each station

sampling depth recorded for each net is the average depth registered by the Benthos Time-Depth Recorder during the hour-long tow. The sampling depths in the example were 0, 60, 243, 510, 995, 1 548, 2 088, 2 316, 3 304 and 3 942 m. Shallower areas of particular interest, e.g., a station in the Mona Passage with a bottom sounding of 481 m, were also sampled in two casts. All methods used in the sampling programme are explained in detail in the earlier reports.

2. SPECIES AND RELATIVE ABUNDANCE

The species identified and the estimated or actual total numbers in all samples combined are listed in Table I. Collections were subsampled routinely by aliquot, usually one tenth to one fiftieth of the volume of specimens, to obtain estimated numbers of the more abundant organisms, e.g., copepods, euphausiids and chaetognaths. Often, however, samples from below approximately 200 m contained relatively few specimens of siphonophores, heteropods, euphausiids, chaetognaths and salps, and total counts were made. These methods yielded numbers of each species filtered from the water during an hour-long tow, which values are strictly comparable from station to station and at the depths reported for all cruises. They thus show distributional ranges, areas of abundance and relative abundance of species.

The most numerous of the metazoan planktonic groups and the most widely distributed vertically were copepods, with chaetognaths ranking next. A complete taxonomic analysis of copepods was outside the scope of the project since approximately 450 species of oceanic calanoids, harpacticoids and cyclopoids have been reported from the Caribbean. Therefore, 20 common species, with broad vertical ranges, were selected for counting, the remainder being lumped as "other Calanoida", "other Harpacticoida" and "other Cyclopoida" (Table I). Although the number of calanoid species is far greater than that of cyclopoids, the latter nearly equalled calanoids in total numbers of individuals, the most numerous cyclopoids, *Farranula carinata* and *Oithona plumifera*, being more than twice as abundant as the top-ranking calanoids, *Clausocalanus furcatus* and *Mormonilla minor*. The Harpacticooida, the smallest group of planktonic copepods, includes the third most numerous form counted, *Microsetella rosea*, previously very poorly known in the Caribbean.

The chaetognath fauna consisted of 15 species prevalent in tropical oceans, five rare bathypelagic forms, *Bathybelos typhlops*, *Eukrohnia hamata*, *E. proboscidea*, *Sagitta megalopthalma* and *S. planctonis*, and two neritic species which are sometimes swept into oceanic waters, *S. helanae* and *S. hispida*. Euphausiids were inadequately sampled by the small, slowly-towed nets but, even so, the list includes 15 new records for the Caribbean Sea. The scarcity of heteropods in the collections suggests that they too were inadequately sampled. The species of siphonophores and salps recorded are all familiar inhabitants of Tropical Surface Water (TSW) and Subtropical Underwater (SUW), with the exception of *Ihlea punctata*, a new record for the Florida Straits and the Caribbean.

Affinity indices, calculated from the results of the final cruise, showed two groups with an index of 0.50. An epipelagic group consists of *Sagitta serratodentata*, *S. enflata*, *Paracalanus aculeatus*, *Clausocalanus furcatus*, *Krohnitta pacifica*, *Diphyes bojani*, *Acrocalanus longicornis* and *Farranula carinata*; species having affinity only with the preceding are *Abylopsis eschscholtzii*, *Undinula vulgaris*, *S. hispida* and *Euchaeta marina*. Bathypelagic species comprising the second group are *Mormonilla minor*, *M. phasma*, *Rhincalanus cornutus*, *Conaea gracilis*, *Sagitta macrocephala* and *Aegisthus aculeatus*; species having affinity only with the preceding are *Eukrohnia fowleri* and *E. bathypelagica*. Mesopelagic species did not emerge as a group from the computer programme.

TABLE I

Relative abundance of species of six zooplanktonic groups studied in the Caribbean Sea and adjacent areas

Group and Species	Total numbers
Siphonophora	
Abylopsis eschscholtzii	13 040
A. tetragona	15 608
Bassia bassensis	4
Ceratocymba leuckartii	1
Chelophyes appendiculata	7 482
Diphyes bojani	14 667
D. dispar	4 213
Eudoxoides mitra	4 250
E. spiralis	1 700
Heteropoda	
Atlanta fusca	1
A. inclinata	20
A. inflata	2
A. peroni	14
Cardiapoda placenta	1
Firoloida desmaresti	46
Protatlanta souleyeti	2
Pterotrachea coronata	1
Copepoda	
Calanoida	
Acrocalanus longicornis	28 856
Clausocalanus furcatus	189 191
Euchaeta marina	82 029
Haloptilus longicornis	50 990
Lucicutia flavicornis	54 219
Mormonilla minor	159 076
M. phasma	14 270
Paracalanus aculeatus	70 543
Rhincalanus cornutus f. *atlantica*	53 206
Scolecithrix danae	22 414
Undinula vulgaris	66 514
Other Calanoida	2 905 723
Harpacticoida	
Aegisthus aculeatus	1 694
Macrosetella gracilis	80 563
Microsetella rosea	270 068
Other Harpacticoida	34 442
Cyclopoida	
Conaea gracilis	45 690
Farranula carinata	412 740
F. gracilis	12 895
Oithona plumifera	491 616
Oncaea mediterranea	56 584
O. venusta	124 782
Other Cyclopoida	2 254 849
Euphausiacea	
Euphausia americana	2 891
E. brevis	4 955
E. gibboides	310
a/*E. hemigibba*	585
E. mutica	1 255
a/*E. pseudogibba*	46
E. tenera	6 789
a/*Nematobrachion boopis*	165
a/*N. flexipes*	179
a/*Nematoscelis megalops*	240
a/*N. microps/atlantica*	406
a/*N. tenella*	260
a/*Stylocheiron abbreviatum*	35
a/*S. affine*	1 720
a/*S. carinatum*	2 845
S. elongatum	5
S. longicorne	2 416
a/*S. suhmii*	875
a/*Thysanopoda aequalis*	461
T. monacantha	6
a/*T. obtusifrons*	230
a/*T. pectinata*	1
a/*T. tricuspidata*	54
Chaetognatha	
Bathybelos typhlops	1
Eukrohnia bathyantarctica	275
E. bathypelagica	270
E. fowleri	195
E. hamata	17
E. proboscidea	5
Krohnitta pacifica	4 762
K. subtilis	3 495
Peterosagitta draco	11 717
Sagitta bipunctata	2 162
S. decipiens	13 183
S. enflata	57 795
S. helanae	14
S. hexaptera	9 545
S. hispida	1 131
S. lyra	3 529
S. macrocephala	471
a/*S. megalopthalma*	2

Group and Species	Total number	Group and Species	Total number
S. minima	165	Salpidae	
S. planctonis	875		
S. serratodentata	31 331	Thalia punctata	1 630
S. zetesios	69	Salpa fusiformis	2 616
		Thalia democratica	25 530
		Weelia cylindrica	6 913

a/ New record for the Caribbean Sea

3. HORIZONTAL AND VERTICAL DISTRIBUTION

We did not find a uniform distribution in abundance either in any group or all considered together. Instead, the greatest numbers were collected in the central Caribbean and the areas of upwelling in the Central American bight. This is best illustrated by the distribution of copepods (Fig. 2), which also indicates a high level of productivity in the eastern Caribbean, suggested by earlier studies, as well as a massing of organisms in the far west as waters approach the Yucatan Channel.

The vertical distribution of all species except very rare forms, e.g., Stylocheiron elongatum, Thysanopoda pectinata, Sagitta planctonis and the heteropods, was diagrammed to show the relationship of abundance to temperature and salinity. Examples are given in Figs. 3 and 4. Many species were found over a great range, the lower extremes of which cannot always be ascribed to contamination because of the frequency of records, and the efforts taken to wash nets and to eliminate desiccated specimens from consideration. However, the depths of major concentrations were usually clearly delimited. Thus the copepods Acrocalanus longicornis and Clausocalanus furcatus (Fig. 3A) live primarily in TSW and SUW, but the former is far more numerous in surface waters than the latter. Euchaeta marina, Paracalanus aculeatus, Scolecithrix danae and Undinula vulgaris are also found mainly in the upper 100 m, and Farranula carinata (Fig. 3D) and F. gracilis are most numerous in sub-surface swarms. Haloptilus longicornis is concentrated between approximately 100 and 250 m, day and night, occurring in lower TSW but most abundant in SUW and upper North Atlantic Central Water (NACW). Lucicutia flavicornis is distributed similarly, except that it is most numerous in TSW. Rhincalanus cornutus f. atlantica was common over a broader range than the others, being rare at the surface, but numerous in TSW and SUW, while the majority were living in NACW and Subantarctic Intermediate Water (SAIW). Others with similar extended distributions are Macrosetella gracilis, Microsetella rosea (Fig. 3C), Oithona plumifera, Oncaea mediterranea and O. venusta. In contrast, Mormonilla minor (Fig. 3B) was one of the few living in great abundance below SUW, common in SAIW and extending into North Atlantic Deep Water (NADW). The distribution of M. phasma, Aegisthus aculeatus and Conaea gracilis is similarly deep and the numbers fewer.

Distributional records of the more frequently caught euphausiid species indicate both migratory and non-migratory habits in that some occurred over a very broad vertical range in comparison with others. Stylocheiron carinatum and S. suhmii were collected only in TSW and SUW, Nematobrachion boopis only in NACW and SAIW, and Nematoscelis tenella in NACW. Those found in TSW, SUW and NACW, but primarily in NACW, are Euphausia hemigibba and Nematobrachion flexipes; those more numerous in TSW were E. americana, E. brevis, E. mutica, E. tenera (also caught in SAIW), Stylocheiron affine, S. longicorne and Thysanopoda aequalis. Another group living mainly in NACW, but also collected in SUW, consists of E. pseudogibba, Nematoscelis megalops, N. microps/atlantica, S. abbreviatum and T. obtusifrons.

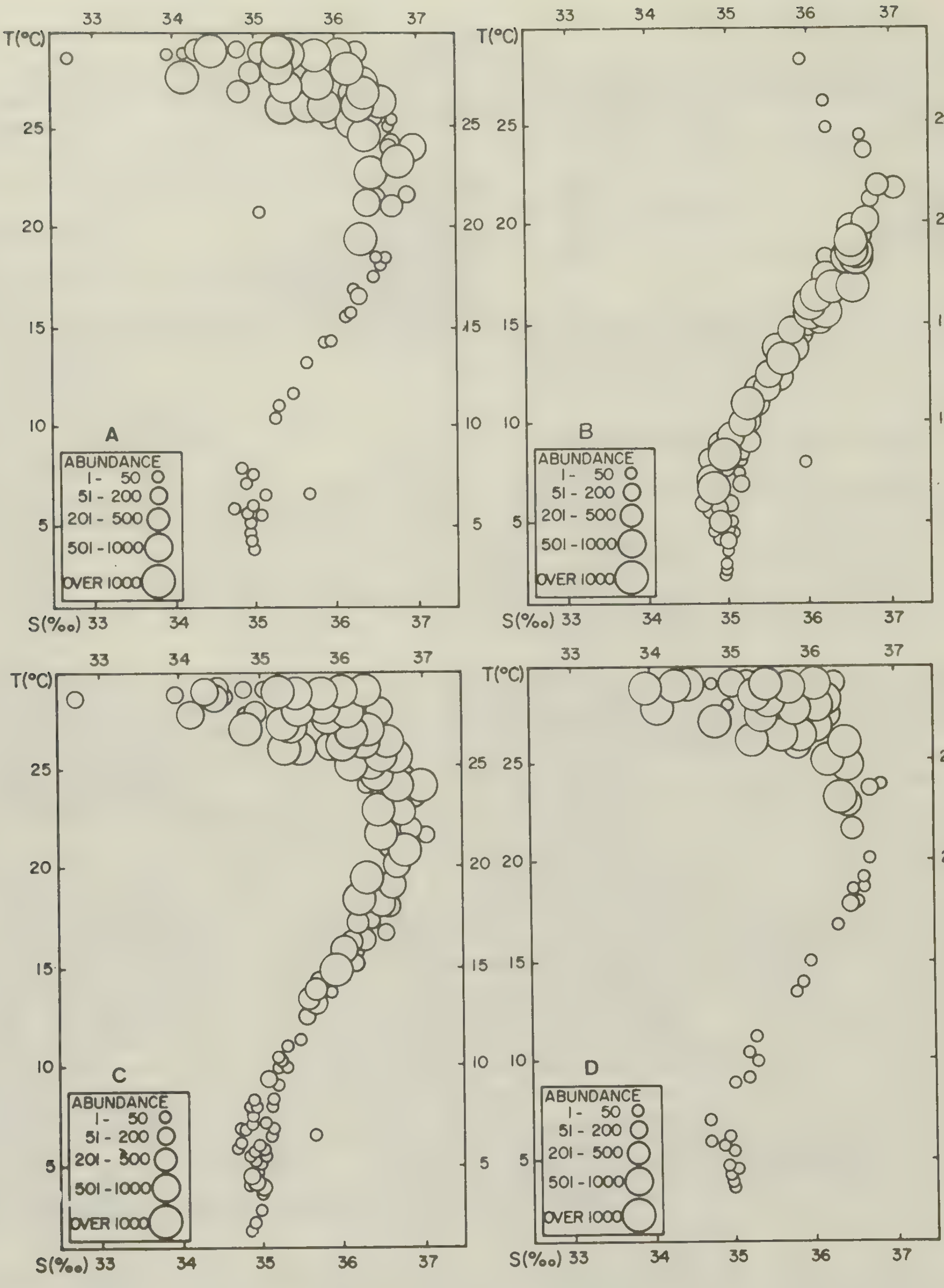

Fig. 3 Temperature-salinity-plankton diagrams. A. Clausocalanus furcatus; B. Mormonilla minor; C. Microsetella rosea; D. Farranula carinata.

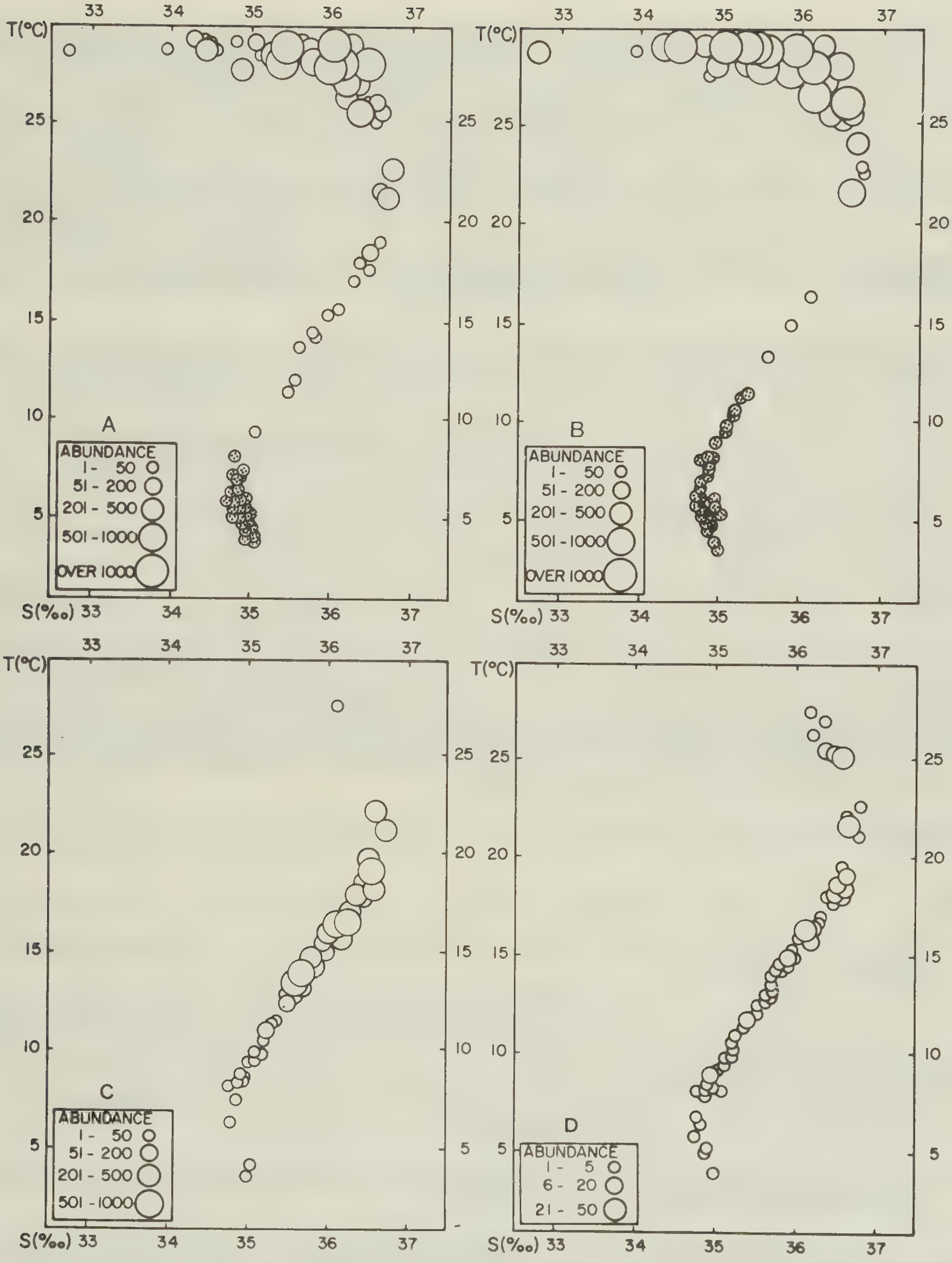

Fig. 4 Temperature-salinity-plankton diagrams. A. Sagitta serratodentata (open circles) and S. macrocephala (stippled circles); B. S. enflata (open circles) and Eukrohnia bathypelagica (stippled circles); C. S. decipiens; D. S. lyra

The vertical distribution of many chaetognath species is also extensive with, however, the major concentrations clearly stratified. Most *Sagitta serratodentata* (Fig. 4A), *S. enflata* (Fig. 4B), *S. bipunctata* and *Krohnitta pacifica* live in warm surface waters of highly variable salinity, while *S. hexaptera* and *Pterosagitta draco* are usually associated with the more saline SUW. The least numerous epipelagic species were *S. hispida*, a natural inhabitant of inshore waters, and *S. minima*, of shelf and slope areas. Below these are four that span the greatest vertical range among chaetognaths in the Caribbean from SUW into SAIW and NADW: *S. decipiens* (Fig. 4C), *S. lyra* (Fig. 4D), *S. zetesios* and *Krohnitta subtilis*. The remaining four of the more abundant species were largely restricted to SAIW and NADW: *Sagitta macrocephala* (Fig. 4A), *Eukrohnia bathyantarctica*, *E. bathypelagica* (Fig. 4B) and *E. fowleri*.

Changes in distribution of some species, primarily copepods and chaetognaths, indicate upwelling, sinking, or admixture of coastal with oceanic waters. *Farranula gracilis* is a likely indicator of warm, saline waters of shallow equatorial origin when it is found in the Caribbean and the Florida Straits. The presence of *Aegisthus aculeatus*, which lives primarily in SAIW and NADW, in shallower water masses, indicates upwelling as does *Mormonilla minor*, if numerous in TSW. Chaetognath species which mark an admixture of coastal waters when found in the open sea are *Sagitta friderici* and *S. tenuis* (not collected during this study), *S. helenae* and *S. hispida*. The presence of deep water species in relatively large numbers at unusually shallow depths indicates upwelling, e.g., *S. lyra*, *S. macrocephala* and *E. bathyantarctica* at 50, 635 and 230 m, respectively, at a station north of Panama. There is also the possibility that chaetognath species, rare in the Caribbean, may be indicators of waters entering the Sea from the North Atlantic, e.g., *Eukrohnia hamata* and *Sagitta planctonis*, known to be established in the North Atlantic, *E. proboscidea*, reported from southeast Africa, and *S. megalopthalma*, from the Mediterranean and the Gulf of Guinea. Locations at which specimens were collected are, in many cases, in or near the Windward and Anegada Passages and those between the Lesser Antilles. Intensive sampling in these areas might well show that there are biological labels to mark the influx of North Atlantic waters at various depths.

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AN INEXPENSIVE CHEMICAL METHOD FOR THE CONTROL AND SYNCHRONOUS INDUCTION OF SPAWNING AND REPRODUCTION IN MOLLUSCAN SPECIES IMPORTANT AS PROTEIN-RICH FOOD RESOURCES

by

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CONTENTS

1. INTRODUCTION
2. RESULTS
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Abstract

We have found conditions under which low concentrations of hydrogen peroxide (added to sea water) will rapidly induce the synchronous and copious spawning of both male and female abalones (Haliotis rufescens), and male and female mussels (Mytilus californianus). We have also characterized the basic pharmacological and physiological mechanism of this effect. This method is directly applicable to both mariculture production, and the genetic management and improvement-breeding, of these protein-rich and highly palatable food resources.

This inexpensive and easily controlled chemical method may offer unique advantages for the control and synchronous induction of spawning in large numbers of animals, in both artificial and natural ponds and mariculture lagoons. Wide applicability to other molluscan species locally important as protein-rich food resources throughout the Caribbean is suggested, and is currently under investigation.

Resumen

En determinadas condiciones, la presencia de H_2O_2 en bajas concentraciones (añadido al agua del mar) induce rápida y sincronizadamente un abundante desove en la oreja de mar (Haliotis rufescens) y los mejillones (Mytilus californianus). Se ha determinado además el mecanismo farmacológico y fisiológico fundamental de ese fenómeno. El método puede aplicarse directamente en maricultura, en trabajos genéticos y para la mejora de la reproducción de estos moluscos alimentarios, ricos en proteínas y muy sabrosos.

Este método químico, poco costoso y fácil de controlar, puede ofrecer numerosas ventajas para el control y la inducción sincronizada del desove en gran número de animales, tanto en estanques artificiales y naturales como en lagunas dedicadas a la maricultura. Las posibilidades de aplicar este método a otras especies de moluscos importantes en algunas zonas del Caribe como fuentes de proteínas están actualmente estudiándose.

1. INTRODUCTION

The development of "mariculture" has, thus far, been unable to increase significantly the availability of low-cost animal protein to the majority of the world population. This is largely because present schemes for the necessary control of reproduction and mortality of the animals under culture are often expensive in absolute terms, in addition to being inflationary (i.e., inefficient). As a result, crustacea and molluscs currently produced by culture are sold, for the most part, as luxury foods unavailable to the bulk of the population.

We have recently discovered (Morse *et al.*, 1976a,b) a general biochemical mechanism by which hydrogen peroxide, added to alkaline seawater, will induce the synchronous and copious spawning of gravid male and female abalones (gastropod mollusc: *Haliotis rufescens*). We have shown that the hydrogen peroxide acts directly to stimulate the enzymatic synthesis of *prostaglandin-endoperoxide* in reproductive tissues of the abalone (and other species) and that the hormone-like prostaglandins formed from this key biosynthetic intermediate, and known to regulate reproduction in higher animals are, apparently, responsible for triggering the physiological spawning response (Morse *et al.*, 1976a,b).

Species of abalone are highly palatable, commercially important food resources in Mexico, U.S.A. and many other parts of the world. However, the significance of our work should extend beyond its application to this single species; we chose to work with this animal, which was available to us locally in California, as a "model system" for the development of a chemical approach to the management of reproduction which may be generally applicable to a wide variety of species. It is our hope that this, or similar inexpensive chemical methods, might offer unique advantages for the economical control of reproduction in large numbers of animals, thus allowing cultivation and management in relatively large and undeveloped ponds and mariculture-lagoons for both human consumption and the genetic improvement-breeding of stock. This method also appears useful for providing essential information of the basic biochemical mechanisms of reproductive control in these and related species of economic importance as protein-rich food resources.

2. RESULTS

As seen in Table I, hydrogen peroxide (H_2O_2) is effective in inducing spawning in both gravid male and female gastropod molluscs (the abalone, *H. rufescens*), and bivalve molluscs (the mussel, *Mytilus californianus*). The effect of H_2O_2 upon the rate of the enzymatic reaction catalyzed by prostaglandin-endoperoxide synthetase ("fatty acid cyclo-oxygenase") from reproductive tissues of the abalone is shown in Fig. 1. Stimulation of this reaction by H_2O_2 appears to be a common property of the enzyme from many organisms and tissues (Morse *et al.*, 1976a,b). We believe that it is this effect which might be directly responsible for the induction of spawning in molluscs, as either H_2O_2 *or* certain prostaglandin products derived from this reaction (see Fig. 2) can induce this result (Morse, 1976a).

The induction of spawning by H_2O_2 is dependent upon both the concentration of H_2O_2 added and the alkalinity of the seawater environment (Table II). This requirement for an alkaline medium apparently reflects the process of base (hydroxide)-catalyzed decomposition of the H_2O_2 to yield an electronically activated, or "free-radical", form of oxygen, which may then participate as a preferred and stimulatory substrate in the enzymatic synthesis of prostaglandin-endoperoxide, as illustrated in Fig. 3 (Morse *et al.*, 1976a). A variety of common oxidizing agents which do not yield electronically activated oxygen do not induce spawning (Table III).

Kikuchi and Uki (1974a) have found that UV-irradiated sea water is capable of inducing spawning in abalones and other molluscs. We consider it likely that this effect is mediated by an oxidative mechanism similar to that which we have characterized (Morse *et al.*, 1976a), although our attempts at analysis of this effect have been hampered by irreproducibility of the UV-induction itself, this in conditions in which animals remain readily inductible with

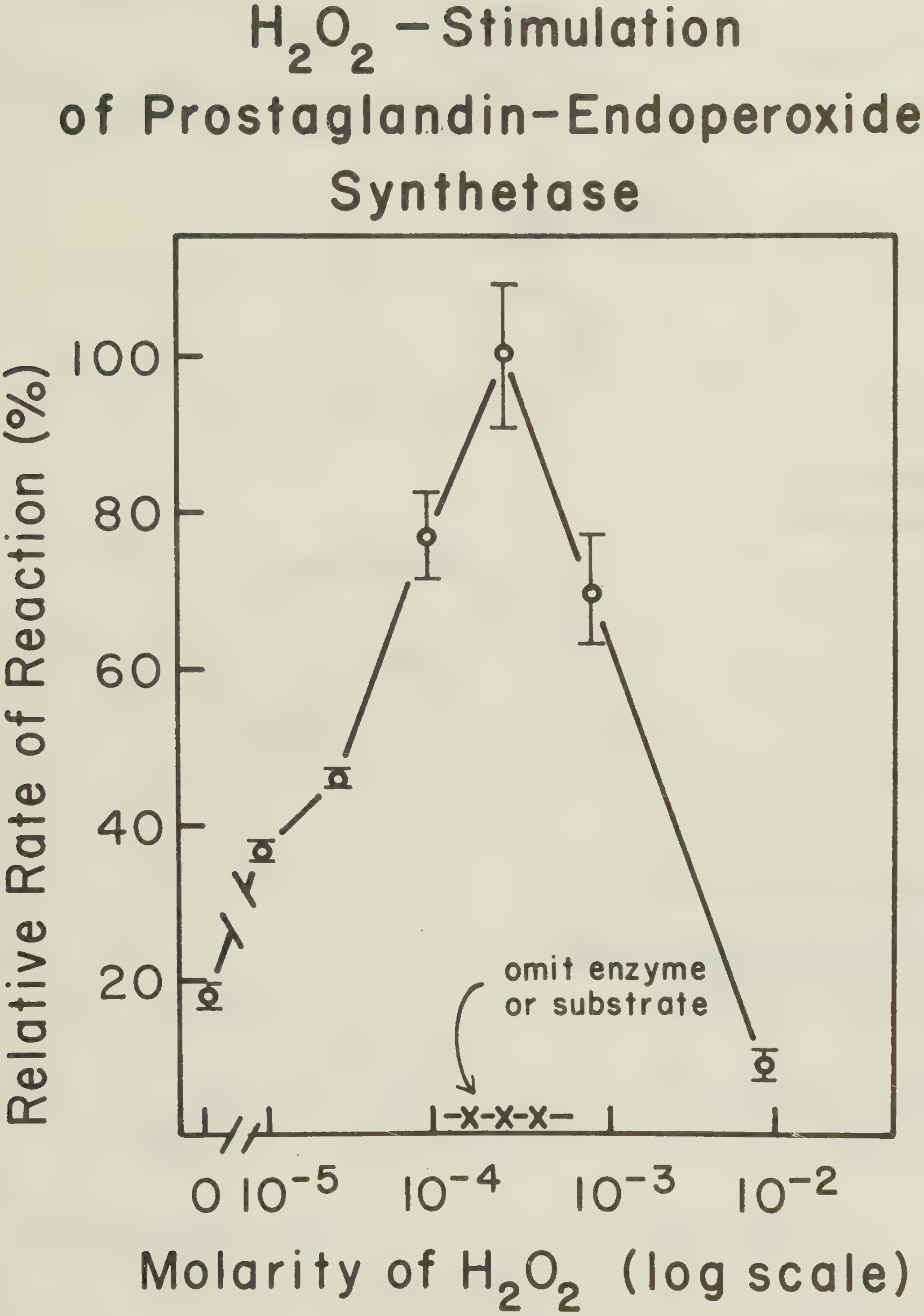


Fig. 1 H_2O_2-stimulation of prostaglandin-endoperoxide synthetase. An extract prepared by homogenization of abalone eggs was assayed for the arachidonic acid-dependent activity of prostaglandin-endoperoxide synthetase as described by Morse et al. (1976a). Determination of this activity as a function of the concentration of exogenously added H_2O_2 reveals maximal stimulation at ca. 3×10^{-4} M H_2O_2. As also shown in this figure, there is virtually no apparent activity in the presence of H_2O_2 if either the abalone extract (enzyme) or arachidonic acid (substrate) is omitted

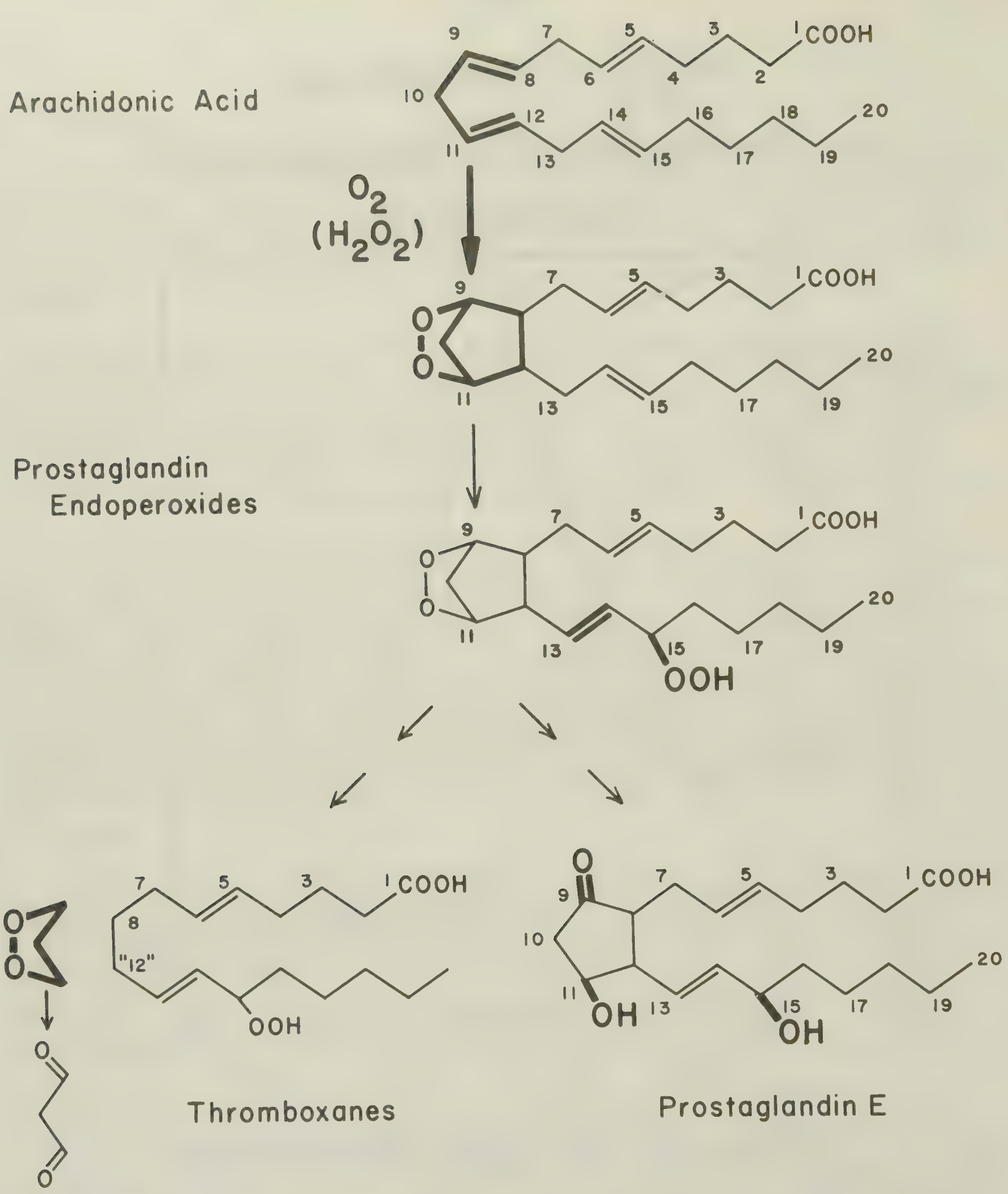
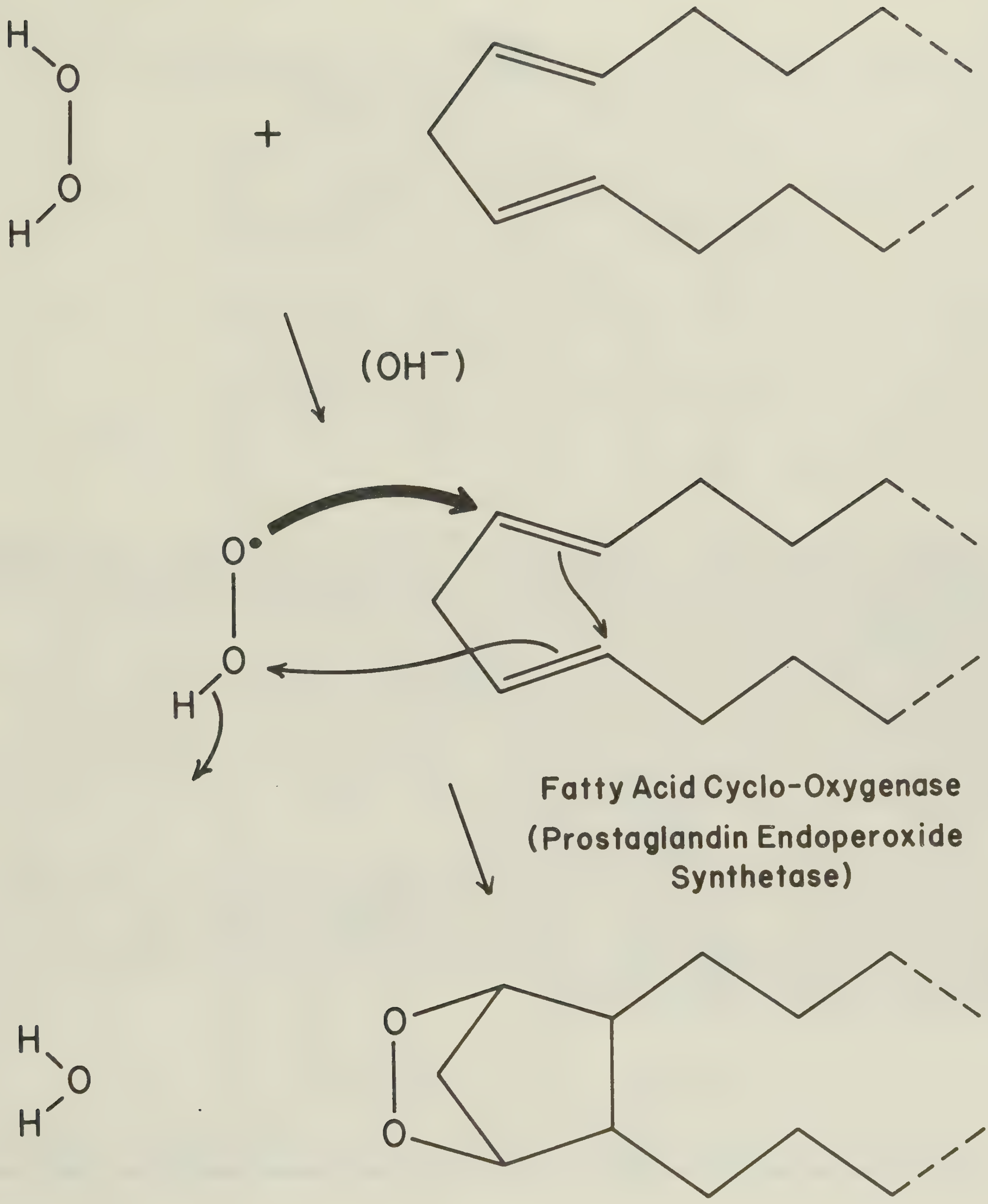

Arachidonic Acid
COOH
O2
(H2O2)
Prostaglandin Endoperoxides
OOH
Thromboxanes
Prostaglandin E
OH
OH

Fig. 2 Enzymatic biosynthesis of the prostaglandin endoperoxides, prostaglandins and thromboxanes. The first introduction of oxygen, catalyzed by the hydrogen peroxide-stimulated fatty acid cyclo-oxygenase, or "prostaglandin-endoperoxide synthetase", is required for cyclization of the linear substrate lipid, arachidonic acid. The instability of the resulting strained-ring endoperoxide provides the driving force for stabilization via either splitting of the dioxy-linkage to yield the keto-hydroxy-prostaglandins, or β-elimination (and subsequent splitting of the dioxy-linkage) to yield the thromboxanes.


H
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+
(OH⁻)
O•
O
H
Fatty Acid Cyclo-Oxygenase
(Prostaglandin Endoperoxide
Synthetase)
H
O
H
O
O

Fig. 3 Diagram of a plausible reaction mechanism for H_2O_2-stimulation of the enzymatic synthesis of prostaglandin endoperoxide (Morse et al., 1976a). Alkali (OH^-)-catalyzed decomposition of hydrogen peroxide, to first yield the highly reactive hydroperoxy free radical, or the peroxy (•OO•) diradical, is suggested. The ability of the enzyme to catalyze the subsequent free radical-mediated attack and induced cyclization of the lipid presumably resides in the unique electronic activity of the copper at the enzyme's active site.

TABLE I

H_2O_2-Induction of spawning in molluscs

	Total Number of Animals	
Abalones:	Tested	Spawned
H_2O	28 (13 F, 15 M)	0
H_2O_2	31 (17 F, 14 M)	30 (16 F, 14 M)
	Total Number of Groups	
Mussels:	Tested	Spawned
H_2O	7	0
H_2O_2	6	6

Animals collected locally from the waters off Santa Barbara, California, were tested in 12-l plastic tubs containing vigorously aerated, fresh running sea water, thermostatically maintained at 13-14°C; this low temperature was found effective in suppressing spontaneous spawning (Morse *et al.*, 1976a). The influx of sea water was carefully adjusted to 100 ml/min/tub, thus resulting in a controlled dilution-rate of 50% per h. After the animals had been pre-equilibrated under these conditions for 1 h, the water in all tubs was buffered at pH 9.1 by the addition of tris-hydroxymethylaminomethane (Tris, 6 mM). Hydrogen peroxide was added from a cold, stabilized 30% stock-solution to yield a final concentration of 5 mM; as a "control" treatment, approximately 50% of the animals tested received an equal volume of fresh water instead of hydrogen peroxide. Concentrations of Tris and H_2O_2 were maintained within ± 33% of the indicated mean values by hourly replenishment for a total of 4 hours, after which these concentrations were allowed to fall steadily as a result of the constant influx of fresh sea water.

Comparably gravid abalone-bedfellows (*Haliotis rufescens*) were incubated individually in separate tubs; all animals which spawned (both female, "F" and male, "M") did so within $3\text{ h} \pm \frac{1}{2}\text{ h}$ after the first addition of H_2O_2. Mussels (*Mytilus californianus*) were incubated in groups of 12/tub; no animals in the control groups spawned, whereas at least 2 females and at least one male in *each* of the H_2O_2-treated groups were observed to spawn within 6-8 hours after the first addition of H_2O_2 after which the dense spawn obscured and prevented further counting of spawning animals.

TABLE II

Concentration-Dependence as a function of alkalinity

Treatment	Female Abalones	
	Tested	Spawned
H_2O (pH = 7.8)	2	0
" + H_2O_2, 0.2 mM	2	0
" " 1.0 mM	2	0
" " 4.2 mM	2	1
Tris (6 mM, pH = 9.1)	2	0
" + H_2O_2, 0.2 mM	2	0
" " 1.0 mM	2	1
" " 4.2 mM	2	2

Comparably gravid female abalones were tested as described in the legend to Table I, except that the mean concentrations of Tris and H_2O_2 were varied as indicated here.

TABLE III

Other oxidants tested

Oxidant (5 mM)	Female Abalones	
	Tested	Spawned
Na – Nitrite	2	0
– Thiosulfate	2	0
– Dichromate	2	0
– Perchlorate	2	0
– Periodate	2	0
– Hypochlorite	4	0
K – Permanganate	2	0

Comparably gravid female abalones were tested as described in the legend to Table I, except that the hydrogen peroxide was replaced by the different oxidants indicated here.

H_2O_2. In this respect, we find that induction of spawning with H_2O_2 is more easily controlled and its absolute reproducibility (Table I) makes it more reliable than induction by UV-irradiation of sea water.

The fertility of abalone gametes obtained by H_2O_2-induction of spawning is, initially, quite high, resulting in >90% fertilization and subsequent larval development under optimal conditions (Table IV). However, this fertility is lost on prolonged exposure of the gametes to H_2O_2, the sperm being more sensitive in this respect than the eggs (Table IV).

We have induced abalones to spawn and release their gametes into water free of H_2O_2 by exposing the animals to Tris (tris-hydroxymethylaminomethane) and H_2O_2 for 135 min., afterwards replacing this medium with fresh sea water; spawning occurred as usual at about 180 min after the first addition of H_2O_2. Sperm and eggs obtained by this procedure exhibited very high fertility and subsequent normal development of planktonic larvae (Tabel V). The dependence of fertilization upon sperm concentration, and the lysis of eggs at very high concentrations of sperm, are similar to those observed by Kikuchi and Uki (1974b). (It is interesting to note that in several spawnings (e.g., Table V), we have observed as much as 6-14% fertilization and normal veliger development under conditions in which exogenous sperm had been rigorously excluded from the females and their eggs. This observation suggests the order of magnitude of a strong selective advantage accruing to the occasionally hermaphroditic abalones, which Murayama (1935) and others had first observed.)

Our method is currently useful for the analysis of gametogenesis and other aspects of reproductive physiology and control, for genetic improvement-breeding and for culturing animals on a limited scale. Extension to the control of reproduction and culture on a large scale should now depend simply upon the development of effective means for the controlled introduction, and subsequent removal (see Table V), of the H_2O_2 (or some similar source of active oxygen). We are currently investigating the feasibility of using various chemical and physical means for the neutralization or removal of the active oxidant after "induction" has occurred, prior to the actual release of gametes.

3. DISCUSSION

The experiments presented in Tables I and V indicate that the method we have described might have wide applicability to the culture of a variety of molluscan species potentially important as economical sources of animal protein. The advantages of using H_2O_2 for the control and synchronous induction of spawning and reproduction in these animals include the reliability and ease of control of the method, as well as its low cost.

The development of practicable schemes for animal culture and mariculture based upon such methods naturally requires concomitant attention to efficient methods of water temperature and quality control, adequate supply of proper foods and habitats and means of harvesting. It is often the restriction of any phase of such an operation to an artificially constructed "hatchery" which results in the costly spiral of capital-intensive measures for control of water-quality, disease and feeding problems which the hatchery itself inevitably causes. In addition, the required transfers of juvenile animals from the hatchery are often costly, both in terms of labour and in terms of mortality of the animals themselves. It is precisely such inflationary inefficiencies, inherent in many present-day mariculture operations, which limit the effectiveness of these operations in providing food where it is most needed, i.e., the resource-depleted, economically "under-developed" areas of the world.

Through the careful choice of organisms and locations for culturing however, it might be possible to bypass some of the serious inefficiencies inherent in the hatchery-type operation, and, with the insurance of proper safeguards against pollution and other forms of spoilage of the aquatic environment, take direct advantage of the self-balancing quality and food-supplies of the shallow-marine ecosystems themselves, for the cultivation of our own food species.

TABLE IV

Fertilization and larval development of abalone gametes as a function of their exposure to H_2O_2

Exposure of sperm	Eggs Fertilized	
	Eggs 5 min in H_2O_2	Eggs 30 min in H_2O_2
1 min in H_2O_2	94%	66%
10 min in H_2O_2	0%	0%

A pair of gravid male and female abalones was induced to spawn in separate tubs as described in the legend to Table I. The gametes were allowed to remain in the presence of Tris and H_2O_2 for the indicated times; the sperm were then "washed" by extensive dilution, and the eggs washed by 2 successive cycles of settling and resuspension in fresh sea water. Fertilization was then tested (at 18°C) by mixing approximately 200 eggs (2 separate samples each) with sperm 2 separate samples each, at a final density of approximately 10^7/ml); after 20 minutes the eggs were washed free from sperm, and allowed to develop in fresh sea water at 18°C. Results were evaluated by microscopic examination 28 h after fertilization, at which time the majority of the fertilized eggs had developed into hatching and free-swiming ciliated trochophore larvae.

TABLE V

Fertilization and larval development with abalone gametes obtained by H_2O_2-induction and subsequent water-change

Added Sperm/ml (approximate)	% of Original Eggs	
	Trochophores at 22 hours	Veligers at 40 hours
0	12	9
10	0 (lysis)	0
10	0 (lysis)	0
10	92	87
10	91	84
10	36	28
10	32	28
10	14	8

A pair of gravid male and female abalones was induced to spawn in separate tubs as described in the legend to Table I, except that the Tris and H_2O_2 were removed by decantation 135 min after the first addition, and replaced with isothermal fresh sea water. The animals spawned, as usual, approximately 45 min later. Eggs (approximately 200 in each test) were incubated 10 min at 18°C in the presence or absence of added sperm as indicated, and then washed and incubated in fresh sea water at 18°C. The number of eggs developing into ciliated, free-swiming trochophores 22 hours after fertilization, and into shell-bearing veliger larvae at 40 hours, was determined in each sample by microscopic examination.

Inexpensive chemical methods, such as we have reported here, might provide efficient means for synchronous control and management of reproduction of these organisms in situ, thus affording further economies through the use of large-scale and relatively "unimproved" mariculture lagoons. It is only on this large scale, which such culture can make possible, that the filter-feeding and herbivorous marine invertebrate animals will be able to yield the economical harvest of inexpensive animal protein they theoretically represent. Wide applicability of our method for the control of reproduction in a variety of molluscan species locally important as protein-rich food resources throughout the Caribbean is suggested, and is currently under investigation.

We are particularly interested in establishing cooperative research and development efforts with local groups in this area, and are most grateful to the organizers of the CICAR II Symposium for providing this opportunity for our first exchange with interested delegations from the participating countries.

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ACTUAL AND POTENTIAL FISH PRODUCTION FROM THE CORALLINE SHELVES OF THE CARIBBEAN SEA

by

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Abstract

Fish communities of the coralline shelves of the Caribbean Sea are mostly exploited by means of fish traps, hook-and-line, seines and gillnets. Antillean fish traps provide most of the catch.

Annual harvests of demersal and neritic pelagic species exceed 15 kg/ha in many coralline areas, but the major oceanic banks and the extensive Nicaragua Honduras shelf are subjected to negligible exploitation. A modified exponential surplus yield analysis of the nearshore Jamaican canoe fishery shows that present techniques produce maximum yields of 41 kg/ha (or 14 000 kg/n.mi^2) and that this is attained by a fishing intensity of 0.032 canoes/ha (11 canoes/n.mi^2). On the basis of computed yield (value) - fishing effort curves for the 24 most important species of reef fish in the Jamaican waters, it is concluded that the adoption of a mesh size of 6.60 cm maximum aperture for Antillean fish traps would increase substantially harvests in areas which are subjected to moderate-to-heavy exploitation.

Technological and educational advances leading to full exploitation of all shelf areas of the coralline Caribbean Sea and the adjacent Bahamas will probably result in the total annual yield of demersal and neritic pelagic species increasing by 250% to about 750 000 t and yields in excess of 1 000 000 t are possible, given intensive exploitation and rational management of reef fish communities.

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Resumen

La explotación de las comunidades pesqueras de los bancos de coral del Mar Caribe se hace sobre todo con nasas de alambre, anzuelo y línea, redes de cerco y redes de enmalle. Las más importantes, desde el punto de vista de la captura, son las nasas de alambra antillanas.

En muchas de las zonas coralinas, la producción anual de especies pelágicas demersales y neríticas es superior a 15 kg/ha, pero en los principales bancos oceánicos y en la amplia plataforma nicaragüense-hondurena el nivel de explotación es insignificante. En un análisis hecho del rendimiento de la pesquería costera jamaicana de canoas se ha hallado que con las técnicas actualmente utilizadas se obtienen rendimientos máximos de 41 kg/ha (o 14 000 kg/n.mi ^{2}), con una intensidad de pesca de 0,032 canoas/ha (11 canoas/n.mi ^{2}). Basándose en el estudio de curvas de rendimiento-esfuerzo de pesca correspondientes a las 24 especies más importantes de peces de arrecife que se encuentra en aguas de Jamaica, se llega a la conclusión de que la adopción de una luz de malla máxima de 6,60 cm en las nasas antillanas permitiría aumentar sustancialmente la producción en zonas donde la explotación varía de moderada a intensa.

Con mejoras tecnológicas y profesionales que permitan explotar plenamente todas las zonas de la plataforma coralina del Mar Caribe y de las Bahamas, se obtendría probablemente un aumento del rendimiento anual total de las especies pelágicas demersales y neríticas del orden del 250 por ciento, con lo que la producción aumentaría a una 750 000 t, y con una explotación intensiva y una regulación racional de las comunidades pesqueras de las arrecifes sería incluso posible obtener cifras superiores a 1 millón de t.

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1. INTRODUCTION

The purpose of this paper is to draw together some major conclusions reached as a result of the 1969-73 phase of investigations of the ODA/UWI Fisheries Ecology Research Project in Jamaica, with particular reference to those results which cast some light on the question of the potential harvest from the coralline shelves of the Caribbean Sea and adjacent areas.

Actively growing coral reefs are present on the eastern shelf of Central America, from Colombia to Yucatan, on the island shelves of the Greater and Lesser Antilles and the Bahamas, on the oceanic banks of the Caribbean and at Bermuda. The continental shelf of Venezuela is influenced by the outfall of the Orinoco and other major rivers and by upwelling along the eastern Venezuelan coast; it has extensive non-coralline areas and harbours fishery resources which differ in many respects from those encountered elsewhere in the region (Simpson and Griffiths, 1967).

On present evidence it is likely that, in terms of fisheries production, the major role of hermatypic corals is related to the concentration of nutrients in the reefs as a result of the constant entrapment of plankton from the oceanic waters washing over the reefs, to the high primary productivity which results from recycling of nutrients within the reef and to the shelter the reefs create for many different organisms. This permits development of greater biomasses than might exist in topographically less-diverse habitats and, consequently, fuller utilization of both primary production and the secondary production of reef-dwelling invertebrates.

Certain areas within the coralline region offer some potential for trawling, particularly for penaeid shrimp. Mackerel, tuna and flying fish are taken from the oceanic pelagic zone and small shoaling clupeids and carangids from the neritic pelagic zone form a small, but significant, part of total landings, particularly in the eastern Caribbean. Apart from these exceptions, almost all the fishing effort in the region is directed toward exploitation of reef fish populations which occupy, or are associated with, the rugged bottom topography. Approximately 180 species of reef fish and invertebrates are known to be marketed by the fishermen and the species of major importance are included in the following families: the herbivorous Acanthuridae and Scaridae, the invertebrate-consuming Holocentridae, Pomadasyidae, Mullidae, Chaetodontidae and Balistidae and the predatory Lutjanidae, Serranidae, Carangidae, Sphyraenidae and Carcharinidae. Spiny lobsters (Palinuridae) are a particularly valuable resource and form the basis of important export industries in a number of countries.

1.1 Fishing Methods

The use of trawls and other nets in coralline tropical seas is precluded, or severely restricted, by the presence of reef-building corals (Munro, 1969, 1973). Even the use of bottom long-lines or traps affixed along the length of a setline is hazardous; the line is liable to become lodged under a coral ledge, resulting in loss of all, or much, of the fishing gear. In most areas, fishing techniques are therefore restricted to the use of individually-buoyed traps or vertical lines.

Traps are the predominant feature of Caribbean reef fisheries. There are three basic traditional Antillean trap designs: Z-shaped or S-shaped, with two entrance funnels, or chevron-shaped (otherwise described as arrowhead-shaped) with a single entrance funnel (Munro, Reeson and Gaut, 1971). The Z-shaped traps are most popular in Jamaica, S-shaped traps most popular in Cuba (Buesa Mas, 1962) and single-funnelled chevron traps are most popular in the eastern Caribbean islands.

Maximum aperture of the wire mesh commonly used in the Caribbean is 2.5-5.0 cm. Traps are usually set individually in depths of 10-50 m and usually are not baited. Baits such as chopped fish, crushed crabs or sea-urchins and fruits are effective in increasing catches if the traps are hauled before the bait is exhausted but, for longer soaks (more than about three days), there is no appreciable advantage in baiting the traps (Munro, 1974).

An analysis of the mode of operation of Antillean fish traps is given by Munro (1974). Primary conclusions are that traditional designs afford very high rates of escapement, the rate of escapement is proportional to the size of inlet funnels and inversely proportional to either the area or the volume within which the fish are contained. A simple mathematical model can be used to describe the processes involved. Escapement from medium-sized (183 x 122 x 61 cm) Z- and S-traps averaged 11-12% per day; over 50% of the fish which entered traps escaped during a 10-15 day soak.

Traps designed specifically for the capture of spiny lobsters (mainly Panulirus argus) are relatively uncommon in the region. Their usage appears to be confined largely to areas where resources of lobsters are relatively great and marketability of trap-caught fish is relatively low, either as a result of low population densities in the coastal regions or as a result of sophisticated market requirements.

Hook-and-line fishing techniques are the second most important method of exploitation of reef fishes in the Caribbean region. Variations in technique appear very nearly to equal the number of proponents of the method. In deeper waters (45-250 m), adequate weight is attached to send the monofilament nylon lines almost vertically to the sea floor. Between three and fifteen hooks (size 4/0-7/0) may be placed on a single line. Electrically-powered or hand-powered reels are merely variants of this technique. They give added efficiency in terms of hauling time and are usually fitted with braided stainless steel line, which gives greater control over the bottom rigs at extreme depths.

Seine nets are frequently used in shallow back-reef areas, bays and harbours, but the catch is often largely of small demersal species and immature reef fish, except where shoaling carangids or clupeids occur. Bottom-set gillnets are gaining popularity in some areas but damage to nets by sharks, or by contact with corals, appears to limit possibilities for development of this technique. Floating gillnets are used fairly extensively for capturing neritic pelagic clupeids and carangids, and would appear to offer opportunities for further development in many areas.

In some islands of the Greater and Lesser Antilles spear fishing is becoming an increasingly important economic activity as a result of socio-economic factors related to under-employment and to the low capital outlay for equipment. In economic terms the method appears most attractive, offering income-earning capacity to otherwise unskilled or impoverished individuals. In terms of rational management of resources, spear fishing activities tend to harvest the oldest, largest, least productive members of the fish community and thus promote the conservation of the stock.

A minor proportion of the reef fish catch results from the use of explosives, fish poisons or intoxicants. In some areas controls over the acquisition of explosives are urgently required (Munro, 1969).

1.2 Landings and Statistics for Caribbean Fisheries

Table I shows a compilation of catch statistics for various shelf areas of the Caribbean. These are derived mostly from FAO (1974), supplemented by details derived from Vidaeus (1969a-c, 1970a-d, 1971), Nascimento and Rojas (1970), Simpson and Griffiths (1967), Juhl (1971), Kawaguchi (1971)) Suarez-Caabro (1973) and Hamblyn (pers.comm.). The Table shows the largest annual catches reported in the decade 1964-73 (landings made by distant-water fleets operating outside the Caribbean have been excluded wherever possible), the estimated area of shelf or oceanic bank, the percentage of oceanic pelagic species in the catch and the harvest of demersal and neritic pelagic species per unit area of shelf. For most countries estimates of landings are highly imprecise and the catch is almost entirely undifferentiated.

Despite the poor statistical base a coherent pattern emerges from this exercise. The calculated yields of shelf-dwelling species are lowest in the Bahamas, on the Central American shelf and the oceanic banks of the south-western Caribbean, but this is probably

TABLE I

Yields of shelf dwelling species (excluding oceanic pelagics) per unit area of shelf in the Caribbean Sea and adjacent coralline regions. Based on greatest reported annual catches in the period 1964-73 and calculated areas of shelf within the 200 m isobath

Shelf	Area of Shelf '000 ha	Largest annual catch '000 t	Year	% oceanic pelagic fish	Catch (kg) per ha of shelf per y
BERMUDA	171	1.0	1972	?	<5.8
BAHAMAS IS. including Cay Sal Bank	18 311	6.1	1973	?	<0.3
TURKS and CAICOS IS. including Mouchoir B.	760	0.7	1973	0	0.9
Silver Bank	298	0	-	0	0
Navidad Bank	77	0	-	0	0
	19 446	6.8	1973	?	<0.3
CUBA	10 287	72.5	1973	?	<7.0
Misteriosa Bank	34	0	-	0	0
Pickle Bank	17	0	-	0	0
CAYMAN IS.	17	+	-	+	?
	10 355	72.5	1973	?	<7.0
MEXICO, E. coast of Yucatan	710	+	-	+	?
BELIZE	694	2.0	1972	+	2.9
GUATEMALA	+	0.3	1967	?	?
HONDURAS	6 937	4.4	1971	?	<0.6
NICARAGUA	5 353	7.9	1973	?	<1.5
COSTA RICA	377	0.8	1972	?	<2.1
PANAMA	1 269	?	-	?	?
	15 340	>15.4	-	?	~1.0
Rosalind Bank	494	0	-	0	0
Thunder Knoll	135	0	-	0	0
Alice Shoal	26	0	-	0	0
Serranilla Bank	99) 137	1.4	1968	0	10.2
Serrana Bank	21)				
Bajo Nuevo	17)				
Quito Sueno Bank	110	?	-	?	?
Roncador Bank	4	?	-	?	?
PROVIDENCIA IS.	27	?	-	?	?
SAN ANDRES and nearby banks	13	?	-	?	?
	946	>1.4	-	?	>1.5
JAMAICA, S. coast and nearby banks	292) 342	4.3) 6.6	1968	6) 11	13.8) 17.2
JAMAICA, N. coast	50)	2.3)	1968	21)	37.0)
Pedro Bank, West	704) 804	+	1974	+	+
Pedro Bank, East	100)	0.756	1974	+	7.6
Morant Bank	17	0.095	1973	+	5.6
Salmon Bank	13	0	-	+	0
	1 176	7.5	-	<11	~5.7
HISPANIOLA	2 640	11.1	1973	?	<4.2
PUERTO RICO and VIRGIN IS., including ST. CROIX	1 183	4.9	1972	12	3.6
	3 823	16.0	-	?	<4.2

Shelf	Area of shelf '000 ha	Largest annual catch '000 t	Year	% oceanic pelagic fish	Catch (kg) per ha of shelf per y
Anguilla Bank; Sombrero Bank (ANGUILLA, ST. MARTIN, ST. BART)	449	?	-	?	?
Saba Bank	225	~0	-	?	~0
St. Kitts Bank (ST. EUSTACIUS, ST. CHRISTOPHER, NEVIS)	77	>1.0	1973	?	~13.0
Barbuda Bank (ANTIGUA, BARBUDA)	336	0.8	1973	?	<2.4
MONSERRAT	9	0.1	1973	>50	<5.6
	1 096	>1.9	-	?	<1.7
GUADELOUPE and MARIE GALANTE	211	4.8	1973	>50	<11.4
DOMINICA	46	0.5	1973	>50	<5.4
MARTINIQUE	127	4.8	1967	59	15.5
ST. LUCIA	55	1.7	1973	50	15.5
BARBADOS	34	4.0	1973	91	10.6
	473	15.8	-	~63	~12.4
ST. VINCENT and Grenadine Bank, including GRENADA	360	2.4	1973	28	4.8
COLOMBIA	3 875	60.8	1968	?	<15.7
NETHERLANDS ANTILLES)		10.0)			
VENEZUELA)	9 087	162.4)176.4	1973	~2	~19.0
TRINIDAD)		13.0)			
	12 962	237.2	-	+	<18.3

Note: + indicates that significant quantities of oceanic pelagic fish are landed, but the magnitude of the landings is unknown.

0 indicates that no significant landings are made

? indicates no information

a result of low fishing effort. The greatest yields per unit area (in the region of 15 kg/ha) are obtained on the Jamaican shelf, in the Windward Islands (particularly Martinique and St. Lucia) and the shelves of Venezuela and Colombia. Other areas such as Pedro Bank, Cuba, Hispaniola, Puerto Rico, the Virgin Islands, some of the Windward Islands and the Leeward Islands give intermediate yields which result from low technological development, difficult marketing conditions, sophisticated consumer preferences, presence of ciguatoxic fishes or orientation toward distant-water fishing.

1.3 The Jamaican Fisheries

A discussion of the comparative productivity of Jamaican fisheries, the nature of the various fisheries and an outline of the organization of the fishing industry is given by Munro and Thompson (1973). A brief recapitulation of the situation is given below.

The fisheries of Jamaica can be divided into three basic groups:

(a) the nearshore fisheries, in which canoes are the basic operating units, and which exploit the fish stocks of the Jamaican shelf and proximal oceanic banks by means of traps, handlines, gillnets, seine nets and by trolling.

(b) the trap fisheries based on offshore islands (cays) at oceanic banks, including Pedro Bank, Morant Bank, Bajo Nuevo, Serranilla Bank and Serrana Bank and at various cays on the Nicaragua-Honduras shelf. These fisheries are serviced by carrier vessels which ply between Jamaica and the cays. The canoes which are used for fishing seldom venture more than fifteen miles from their island bases and fishing gears other than traps are seldom used.

(c) the offshore fisheries, which exist only in embryonic form. These fisheries will be based on decked fishing vessels operating on oceanic banks and shelves remote from any land bases. The evidence available at the present time suggests that economically-viable fisheries in offshore areas will have to be based upon stackable trap catches (Munro, 1973) supplemented by high-quality handline and trolling catches.

Statistical information on landings and fishing effort in these fisheries is very poorly based. The most recent survey of landings by the nearshore fishery was in 1968 (reported on by Vidaeus, 1970a), when the estimated total catch of neritic pelagic and demersal species (including crustaceans) amounted to 5 893 metric tons. In addition, about 740 metric tons of oceanic pelagic species were landed. Estimates, supplied to the author by officers of the Fisheries Division of the Jamaican Ministry of Agriculture, show that the carrier vessels servicing fisheries at offshore cays landed about 3 650 metric tons in 1973. Of this total, about 680 metric tons originated from the Pedro cays fishery, about 95 metric tons from the Morant cays and about 2 870 tons from the cays on the Nicaragua-Honduras shelf and adjacent banks. A more recent estimate (1974) by Mr. E.L. Hamblyn (U.K. Ministry of Overseas Development, Fisheries Adviser in Jamaica) indicates that landings by the Pedro cays fishery currently amount to 756 t/year. In addition to the foregoing, about 300 t/year are said to be landed by vessels engaged in offshore operations. Total landings by the Jamaican fishing industry probably therefore amount to about 10 000-11 000 t/year. The 1968 survey of the nearshore fishery indicated that trap-caught demersal species probably contribute about 65% of the total neritic catch (excluding oceanic pelagic species) and that about 20% is taken in seine nets and gillnets. The remaining 15% is taken on handlines; a very small fraction is caught by spear fishermen.

2. ASSESSMENT OF POTENTIAL HARVEST

2.1 An Exponential Surplus Yield Model of the Jamaican Nearshore Fishery

The full results of the 1968 survey have not been released and few details are available other than those released to Vidaeus (1970a). Table II has been compiled to show the 1968 shelf landings of demersal and neritic pelagic species (excluding oceanic pelagic species), the shelf areas adjacent to each Jamaican parish (data for Kingston and St. Andrew, St. Catherine, Clarendon, Manchester and St. Elizabeth, which abut the South Jamaica Shelf have been combined), and numbers of canoes operating on the shelf. Numbers of canoes operating on the shelf of each parish have been derived by subtracting from the total number of canoes the estimated portion of the effort by mechanized canoes applied to fishing for oceanic pelagic species. In all cases the resulting adjustment is very small. The last three columns of Table II show the estimated landings of demersal and neritic pelagic species of each parish, the calculated landings per canoe per year and the calculated landings per unit area of shelf. The reported production and calculated rate of production in the parish of Trelawney appears to be greatly inflated but there is not sufficient detail available to establish the source of the presumed errors.

If it can be assumed that the ecological régimes do not differ substantially around the island, then the relationships between catch per canoe per year and the fishing intensity, expressed as canoes/km^2 of shelf of each Jamaican parish, might be expected on theoretical grounds (e.g., Fox, 1970) to show an exponential relationship. Figure 1a shows a semi-logarithmic plot of the data. This approach differs from previous treatments of surplus

TABLE II

Yields of shelf-dwelling species (excluding oceanic pelagics) per unit area of the Jamaican shelf and proximal banks (but excluding Pedro and Morant Banks). Based upon reported catches for 1968 (Vidaeus, 1970b)

	Area of shelf and proximal banks km^2	Number of canoes	Number of mechanized canoes	% of oceanic pelagic fishes	Effective canoe effort on shelf	Effective canoes per km^2	Total shelf landings (1968) kg x '000	Kg per canoe per year	Kg of neritic species per ha per year
	X	A	B	C	D=A-(BC/100)	E=D/X	F	F/D	F/100X
St. Thomas	165	272	68	7.8	267	1.63	632	2 367	38.4
Kingston and St. Andrew, St. Catherine, Clarendon, Manchester and St. Elizabeth	2 760	1 079	656	5.4	1 044	0.38	3 423	3 279	12.4
Westmoreland	154	484	113	7.4	476	3.09	670	1 407	43.4
Hanover	48	295	54	46.5	270	5.63	150	556	31.2
St. James	34	152	21	0.9	152	4.43	148	974	43.2
Trelawney	31	177	21	34.6	170	5.51	222	1 306	71.9
St. Ann	51	236	17	1.8	236	4.58	133	564	25.9
St. Mary	48	210	59	13.2	202	4.20	155	767	32.3
Portland	130	204	39	31.1	192	1.49	360	1 875	27.6
South coast (St. Thomas to St. Elizabeth)	2 925	1 351	724	5.8	1 309	0.48	4 055	3 098	13.9
North coast (Westmoreland to Portland)	497	1 758	323	21.1	1 690	3.41	1 838	1 082	37.0
All areas	3 422	3 109	1 047	11.2	2 992	0.87	5 893	1 970	17.2

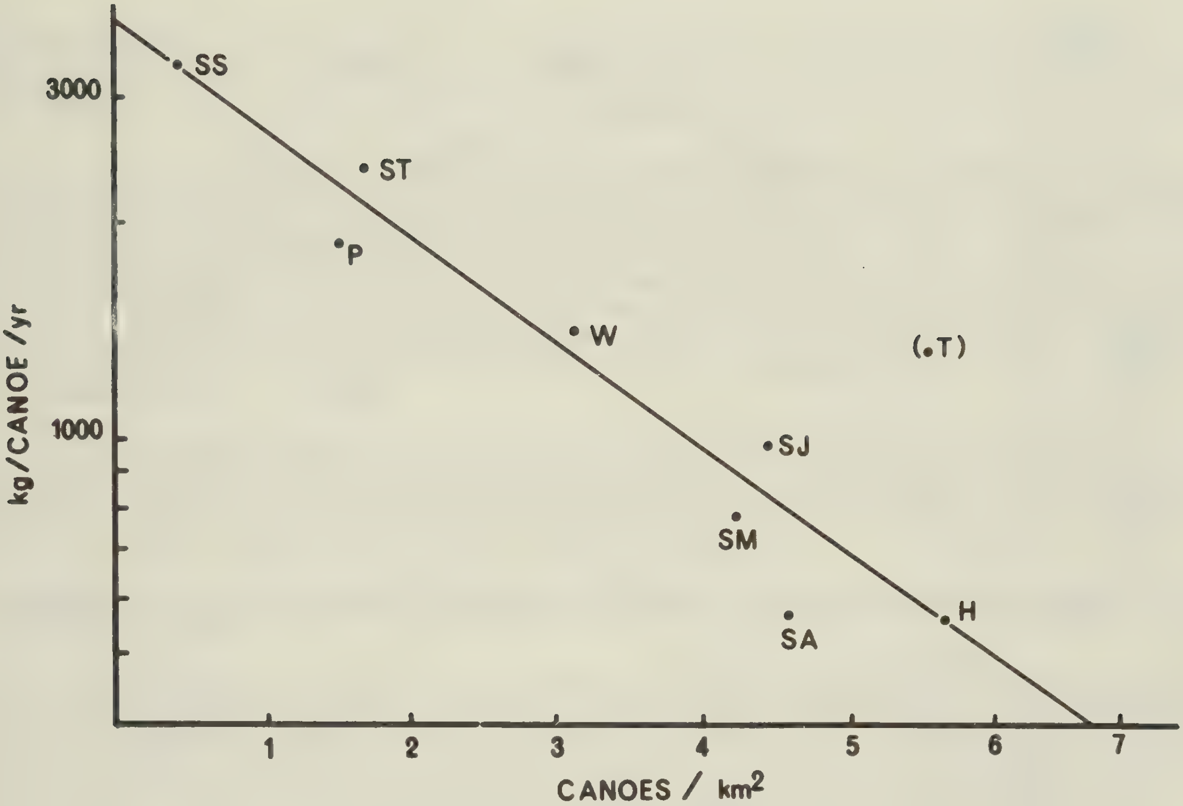

Fig. 1a Semi-logarithmic plot of relationships between annual catches of demersal and neritic pelagic species per unit of effort (kg/canoe/year) and fishing intensity (canoes/km ^{2}) for shelf areas adjacent to the Jamaican parishes of St. Thomas (ST), Portland (P), Westmoreland (W), St. James (SJ), St. Mary (SM), St. Ann (SA), Trelawney (T) and Hanover (H) and from the South Jamaica Shelf (SS). Trelawney is excluded from the regression

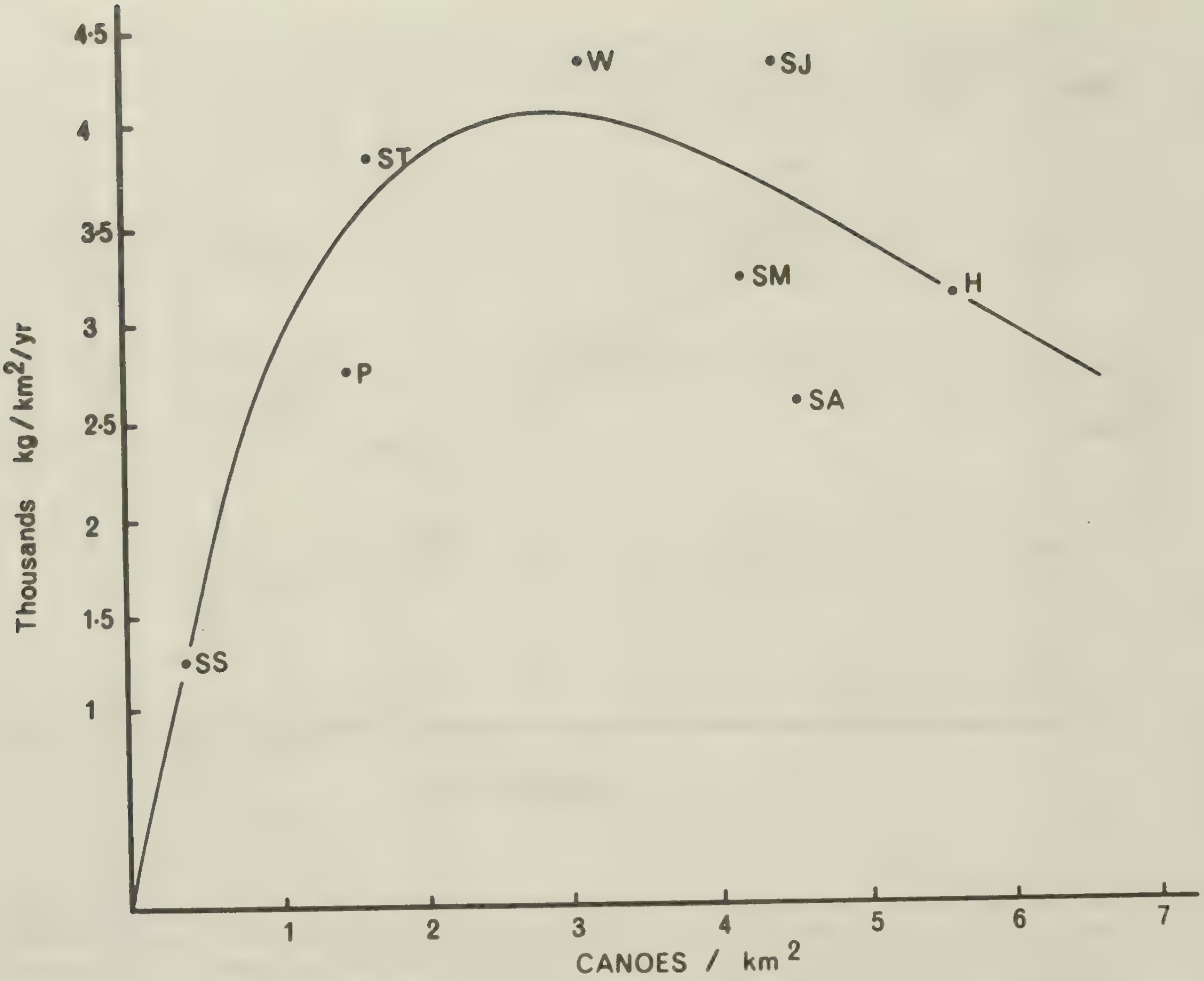

Fig. 1b Regression line of Fig. 1a translated to terms of annual yield per unit area (thousands of kg/km^2/year) relative to fishing intensity (canoes/km^2). Actual yields and fishing intensities (1968 statistics) for shelf areas adjacent to Jamaican parishes and for the South Jamaican Shelf are also included (abbreviations as given for Fig. 1a).

yield models in the use of catch rates from different areas in which the fishing effort differs, instead of the conventional use of annual catch data accumulated during the history of a fishery.

The relatively good fit of the points to the regression (Fig. 1a) appears to bear out these assumptions and suggests that the data can be transformed to give a first estimate of the surplus yield. This is done by simply translating the regression line to terms of production per km^2 per year relative to fishing intensity (canoes/km^2). Fig. 1b shows the result and suggests that with the present fishing methods, maximum yields of around 4 100 kg/km^2 are attained by a fishing intensity of about 3.2 canoes/km^2. The graph also implies that economic factors, such as the high operating costs of outboard motors or poor marketing facilities, limit production on the South Jamaica Shelf, where fishing intensity averages only 0.4 canoes/km^2.

It appears highly unlikely that a yield of 4 100/km^2 is the maximum attainable, as this is largely achieved by fishing with small-meshed (3.30 cm) fish traps supplemented by small-meshed beach seines and gillnets and by handlines. If larger mesh sizes were introduced, greater yields per unit area might be attainable.

2.2 Estimates of Relative Yields from the Trap Fishery, using the Beverton and Holt Stochastic Model

Problems encountered in applying the Beverton and Holt (1957) stochastic model to the fish community exploited by traps in Jamaican waters have been discussed at some length in two previous publications (Munro, 1975, a).Assessments were made of relative total values of harvests of the 24 species which comprise the bulk of the trap fishery landings in two areas (the South Jamaica Shelf and Pedro Bank), given the use of traps with mesh sizes between 3.30 cm and 14.86 cm maximum aperture and at fishing intensities of up to 4.0 canoes/km^2.

One hundred and thirty species of fish occurred in samples taken during the investigations of the ODA/UWI Fisheries Ecology Research Project; most of these species were captured, at least occasionally, in traps. However, catch analyses show that, in most areas investigated, fewer than 25 species comprised over 80% by weight of the total catch. With some exceptions, the species selected for inclusion in the assessment were those for which estimates of biological parameters (in many cases very poorly based) are available, which are marketable and which comprised more than 1.5% of the weight of the trap catch in any area. These areas included the Port Royal reefs, California Bank, the South Jamaica Shelf, the Pedro Cays area and the various unexploited section of Pedro Bank.

The species thus included in this analysis are as follows:

Serranidae Cephalopholis fulva, Epinephelus striatus, E. guttatus, Mycteroperca venenosa
Carangidae Caranx ruber, C. bartholomaei
Lutjanidae Lutjanus apodus, Ocyurus chrysurus
Pomadasyidae Haemulon flavolineatum, H. melanurum, H. album, H. plumieri, H. sciurus, H. aurolineatum
Mullidae Mulloidichthys martinicus, Pseudupeneus maculatus
Scaridae Scarus taeniopterus, Sparisoma chrysopterum, Sp. aurofrenatum, Sp. viride
Acanthuridae Acanthurus coeruleus, A. chirurgus, A. bahianus
Balistidae Balistes vetula

These species comprise 52%-65% of total trap catches at stations on the Jamaica Shelf and 66%-82% of catches at Pedro Bank.

Summations of yield (by value) curves for the 24 species, and including all mesh sizes, are shown in Figs. 2 and 3, which refer respectively to the stocks of the Jamaica Shelf and of Pedro Bank.

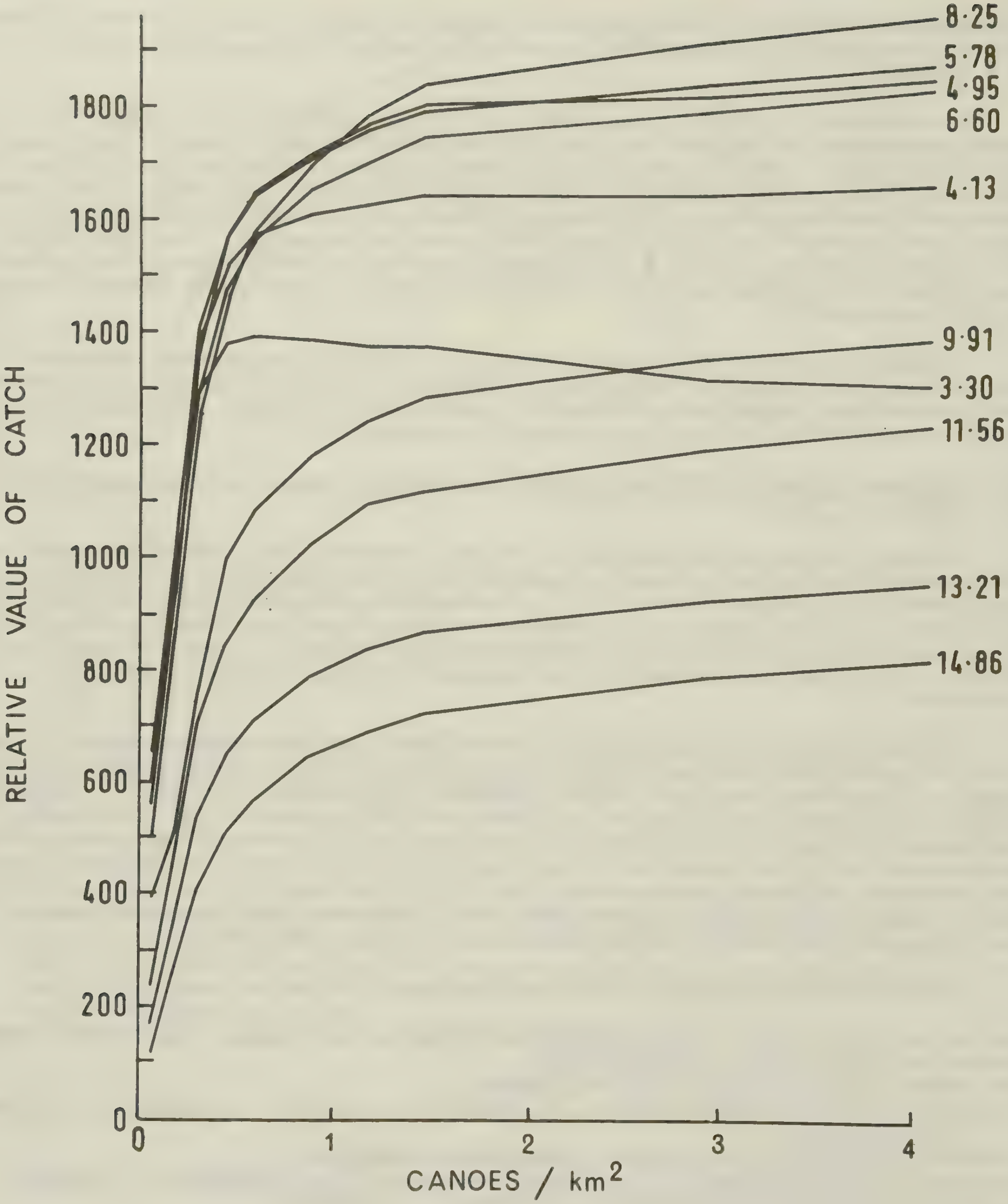

Fig. 2 Calculated relative total values of trap catches of 22 species of reef fish in various mesh sizes (cm maximum aperture) and at various fishing intensities on the South Jamaica Shelf

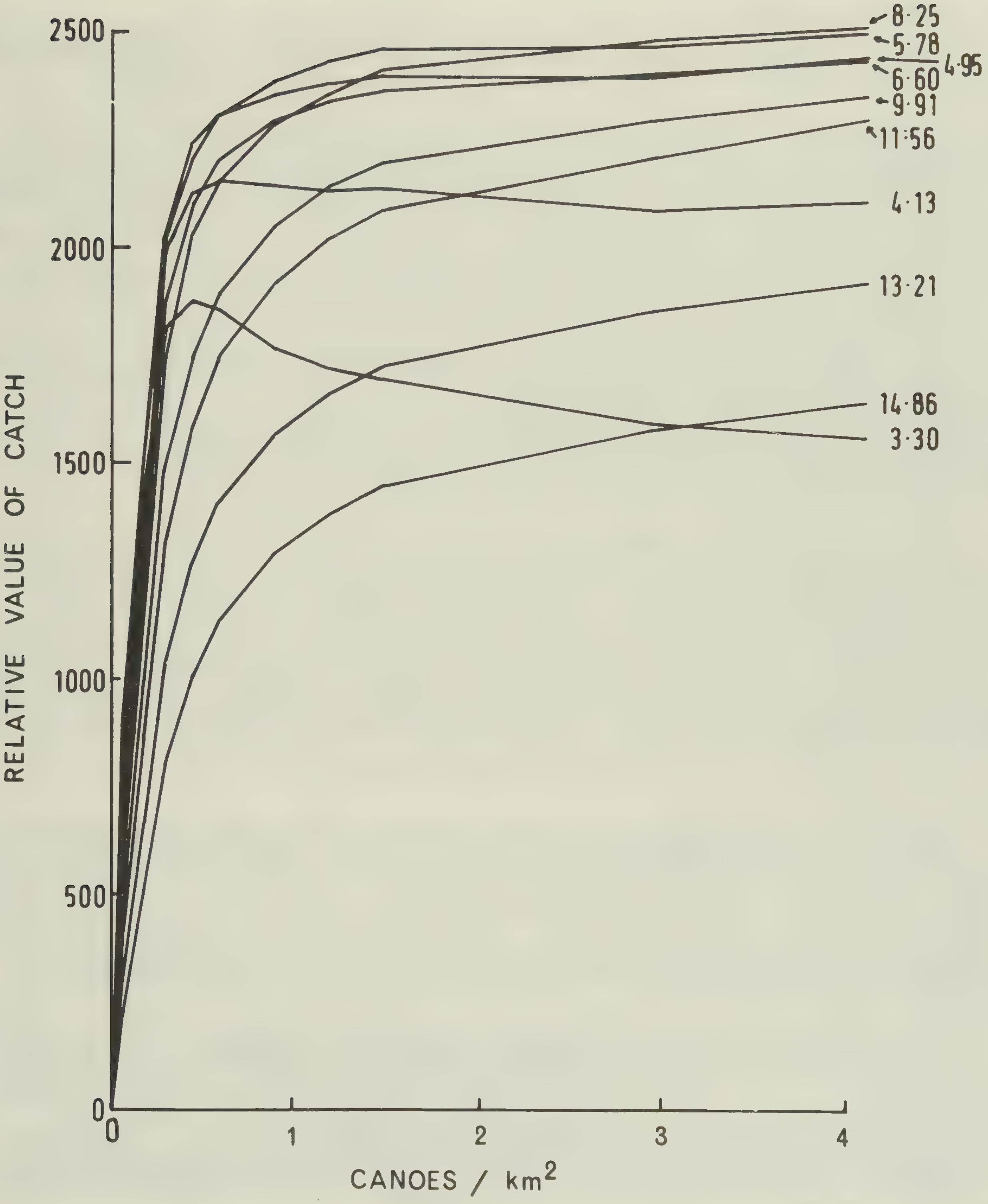

Fig. 3 Calculated relative total values of trap catches of 21 species of reef fishes in various mesh sizes (cm maximum aperture) and at various fishing intensities at Pedro Bank

2.2.1 The Jamaica Shelf

The expected relative value of catches using various mesh sizes at fishing intensities of up to 4.0 canoes/km^2 is shown in Fig. 2. Two points are immediately apparent:

(a) Increases in the value of the total catch, Y_V, can be achieved by adoption of mesh sizes larger than the 3.30 cm and 4.13 cm mesh commonly used in the present fishery. The 3.30 cm mesh is mostly used on the intensively exploited narrow northern shelf, while the 4.13 cm mesh is commonest on the more extensive South Jamaica Shelf. However, the average fishing effort on the South Jamaica Shelf is only 0.4 canoes/km^2, and the increases in Y_V which could be achieved by adoption of 4.95 cm or 5.78 cm mesh are, in themselves, insufficient to warrant a change in mesh size. On the intensively exploited north coast, the fishing intensity averages 3.4 canoes/km^2 and increases in Y_V of 40% to 53% can be achieved by the adoption of a mesh size of between 4.95 cm and 8.25 cm maximum aperture.

(b) The Y_V curves tend to flatten out at when fishing intensity reaches about 1.5 canoes/km^2 and any increase in effort beyond this point results in negligible increases in the total value of the catch and substantial reductions in the value of the annual catch per canoe. Conversely any reduction in fishing effort in the heavily exploited areas will result in large increases in the profit accruing to the remaining fishermen. The relative importance of various species changes in varying degrees both in response to changes in mesh size and in response to increases in fishing effort.

When mesh sizes are increased, yields from a given fishing effort tend to increase for those species with relatively large maximum sizes; but yields of small species decline abruptly and some species disappear from the catches when mesh aperture exceeds maximum body depth attained by the species. The groupers *E. guttatus* and *C. fulva*, the white grunt *H. plumieri* and the trigger fish *B. vetula* are representative of the first group. In contrast, the maximum yields of goatfish , *M. martinicus* and *P. maculatus*, are obtained in the 4.13 cm and 4.95 cm mesh; yields decline in larger mesh sizes and they are eliminated from catches in meshes of greater than 6.60 cm maximum aperture. Munro (1975a) concluded that traps with a mesh size of 6.60 cm would best suit the needs of the Jamaican nearshore fisheries.

2.2.2 Pedro Bank

The relative yields attainable in various mesh sizes at Pedro Bank are shown in Fig. 3. The essential features are similar to those described for the Jamaica Shelf fishery but, owing to the relatively greater abundance of large species (particularly *B. vetula*), differences between yields in large and small-meshed traps are greater and total relative values of catches are also proportionately greater. The curves suggest that yields in mesh sizes between 4.13 cm and 8.25 cm maximum aperture will become nearly stable at fishing intensities exceeding 1.5 canoes/km^2 and the greatest yields will be taken in mesh sizes of 4.95-8.25 cm maximum aperture.

The most important species in the Pedro Bank fishery is *B. vetula*, which will comprise about 25% of the value of the total catch, even in the smallest mesh sizes, and almost 40% in the 8.25 cm mesh. Other species of major potential importance include the French grunt, *H. flavolineatum*, which is extremely abundant in some areas, the goatfishes, *M. martinicus* and *P. maculatus*, the white grunt, *H. plumieri* and the hinds, *E. guttatus* and *C. fulva*. Owing to their relatively great body depth, the surgeon fish, particularly *A. bahianus*, are favoured by moderately large mesh sizes. A 6.60 cm mesh size for traps was also recommended for this fishery (Munro, 1975a).

2.3 Estimation of Potential Harvests from Jamaican Waters

The yield-fishing effort curves shown in Figs. 2 and 3 serve only to show the mesh sizes which may be used in the trap fishery, and to illustrate the relative increases or decreases in yield that will result from changes in mesh size. They do not provide any information on magnitude of catches which might be taken from a given area, and estimates of potential harvests can only be derived indirectly from other data.

2.3.1 The South Jamaica Shelf

Table II shows that the fishing intensity on the South Jamaica Shelf in 1968 was 0.38 canoes/km^2. However, there is reason to believe that, owing to the relatively high proportion of mechanized canoes, the effective fishing effort is actually somewhat in excess of this value. Traps with 4.13 cm mesh are the predominant fishing gear. The 1968 harvest of all neritic species amounted to 1 240 kg/km^2/year, or 3 279 kg/canoe, of which about 60%-70% was taken in traps. The harvest of trap-caught fish amounted therefore to about 800 kg/km^2/year. Fig. 2 shows that an increase to a mesh size of 4.95-8.25 cm could only produce a 5% increase in the harvest, to about 850 kg/km^2. However, if recruitment patterns were enhanced as a result of an increase in the stock of fish which were able to mature before recruitment (Munro, 1975a) then further substantial increases in recruitment might occur. If recruitment were restored to levels similar to those which prevail on Pedro Bank (Munro, 1975a), a 50% increase in harvests to about 1 200 kg/km^2 might be attainable. The potential harvest in traps from a fishing intensity of about 0.4 canoes/km^2 therefore lies probably between 800 kg/km^2 and 1 200 kg/km^2, to which must be added about 440 kg/km^2 of species captured by other methods. The extent to which the latter figure can be increased is unknown. Some increases in handline catches of groupers, snappers and jacks might result indirectly from an increase in mesh size. At present, small blackfin snapper (L. buccanella), which reside on the sill reefs in their juvenile stages, are harvested by small meshed traps at sizes well before maturity. An increase in mesh size would enable more recruits to enter the handline fishery for adult stocks on the deep reef slope, and thus enhance harvest rates. Fig. 2 suggests some increases in the catch would result from increasing effort up to about 1.5 canoes/km^2; but it seems likely that increases in effective fishing effort will only be achieved by radical departures from present fishing practices, including introduction of economical diesel-powered canoes or other small craft, the use of line haulers and more efficient and cheaper traps, improved marketing systems and technological innovations. An effective doubling of effort as a result of such innovations seems not to be impracticable. Development of the fishery for neritic pelagic clupeids (mainly Harengula spp.) and carangids (mainly Selar crumenophthalmus) might also result in increases in the total.

On a conservative basis it is therefore estimated that potential yields might lie between 1 240-1 640 kg/km^2/year. The total area of the South Jamaica Shelf is 2 760 km^2 and the total potential catch from the area is therefore 3 400-4 600 t.

2.3.2 The Northern, Eastern and Western Shelves of Jamaica

Assessment of the potential harvests from the narrow shelves bounding the north, east and west coasts of Jamaica is more problematical than for the South Jamaica Shelf. Details of relative abundances of recruits are not available; owing to the fact that stock densities are reduced to such low levels by the fishery, statistically-adequate samples of the stocks are almost impossible to obtain. Nevertheless, if it is assumed that the composition of the recruits is similar to that estimated for the South Jamaica Shelf, then the yield-value curves shown in Fig. 2 can be applied.

Fishing effort in this area ranges between 1.49 and 5.63 canoes/km^2, with an average over the 662 km^2 area of 3.07 canoes/km^2. Traps with a 3.30 cm mesh are used to produce about 60% of the harvest of neritic species.

Fig. 3 shows that, if 8.25 cm mesh were adopted, the value of the catch would increase by 45%; the corresponding increase in weight would be 75%. The difference between increase in weight and increase in value is because much of the increase in weight would be derived from low-priced species, particularly B. vetula.

Fig. 1 shows that the greatest harvest per unit area which is taken by present fishing methods amounts to about 4 100 kg/km^2. About 60% or 2 450 kg/km^2, is derived from trap-fishing, the remaining 1 650 kg/km^2 from handline fishing, seine nets and gillnets. If a 75% increase in the trap catch be possible as a result of an increase in mesh size, the potential harvest would be about 4 300 kg/km^2 from traps and a further 1 650 kg/km^2 by other methods; 5 950 kg/km^2 in total. This value is 3.3-4.3 times greater than that estimated for the South Jamaica Shelf. The total potential harvest from the 662 km^2 of this shelf is thus about 3 900 t, to which could be added any potential increase in the harvest of species taken in gear other than traps.

Reasons for the high potential yield include possibly the greater productivity of these shelves, which are almost entirely covered by actively growing coral reefs, and greater concentrations of recruits within a given area. This also suggests that the fit of the point pertaining to the South Jamaica Shelf in the regression in Fig. 1a is fortuitous, and likewise suggests that the fishing effort on the South Jamaica Shelf is effectively greater than 0.38 canoes/km^2, owing to the high proportion of mechanized canoes.

Yields of about 80 kg/ha are theoretically possible if recruitment be enhanced as a result of an increase in mesh size.

2.3.3 The Pedro Cays fishery

According to estimates made by Mr. E.L. Hamblyn (pers.comm.) an average of about 72 canoes operated from the Pedro Cays during 1974. As the area within normal range of these vessels is 1 000 km^2, the average fishing intensity is 0.07 canoes/km^2. In the immediate vicinity of the cays, the effort is estimated to be about 0.15 canoes/km^2. Fig. 3 shows that substantial increases in effort are required before maximum sustainable yields are attained. It has also been shown (Munro, 1975a) that the theoretical initial catch per canoe amounts to 10 824 kg/year; this accords very well with the estimate of E.L. Hamblyn that 72 canoes operating from the Pedro Cays have an annual landing of 756 t, equivalent to 10 500 kg/canoe or 760 kg/km^2.

Fig. 3 shows that any increases in fishing effort from the present relatively low levels will result in substantial increases in the harvest. Increasing fishing intensity to 0.15 canoes/km^2 would result in a 40% increase in yield to 1 050 kg/km^2; if the effort were raised to 0.3 canoes/km^2 the harvest would be nearly doubled and production would be 1 450 kg/km^2. The total annual harvest would approach 1 500 t. However, even an increase in the cays-based canoe fleet to 150 vessels, giving an effective fishing effort of only 0.15 canoes/km^2, would require 300-450 fishermen to be based on the cays. This could pose fairly difficult sociological and health problems and this appears to be the major constraint on further development of the fishery. Inhospitable living conditions at the cays and the lack of major financial incentives offered to the fishermen by carrier vessel operators are also important factors. The only alternative means of increasing fishing effort is by way of technological innovations leading to increased efficiency. Constraints on landings from this fishery are therefore socio-economic and technological, and do not relate to fish stocks.

These conclusions probably apply equally to the fishery based at the Morant Cays and the 170 km^2 of banks could therefore be expected to produce a maximum harvest of about 1 450 kg/km^2/year, or a total of 250 t/year.

2.3.4 The Pedro Bank (excluding the Pedro Cays area) trap fishery

This area, which includes all the area remote from the Pedro Cays and beyond the operating range of outboard-powered canoes, is presently virtually unexploited. Only one vessel (the LADY BLYTHE) fished in this 7 000 km^2 area during the time investigations were in progress; it was reputed to land about 100 t/year, caught mostly, if not exclusively, in traps. In addition, canoes from the mainland occasionally venture to the northern edge of the bank when conditions are suitable. Total harvest therefore probably does not exceed 150 000 kg/year, or about 21 kg/km^2 – a negligible amount by any standards.

At present there are no indications that further vessels intend to enter this fishery. It appears likely the profitability of fishing the bank with traditional Z-traps in the manner adopted by the LADY BLYTHE (see Munro and Thompson, 1973) compares unfavourably with the potential profits which can be derived from operating carrier vessels serving the cays fishery. Stackable fish traps developed during the present investigations (Munro, 1973) provide a solution to this, but their adoption for commercial use on Pedro Bank appears unlikely until such time as competition within the cays fisheries induces entrepreneurs to seek greater profits in offshore areas.

Analyses of the composition of trap catches made during these investigations have shown that the relative availability of commercially-important species is quite variable over the bank as a whole. The central portions of the bank in depths of 30-40 m, and remote from the sill reefs which fringe the edges, are comparatively sterile and produce very low trap catches. This area covers about 2 750 km^2. In contrast, the sill reef areas, particularly along the southern edge of the bank from Banner Reef to the south-western tip, are highly productive, as is the entire portion of the bank lying to the east of the Pedro Cays. The northern and western edges have been shown to be rather variable, with catches at a given station ranging from spectacularly high values on occasions to negligible amounts at other times. The calculated average catch rates (with effort standardized in terms of the catch of 1 000 baited hexagonal traps (Munro, 1973) set for one night) are as follows:

Eastern Pedro Bank	3 054)	
Southern Pedro Bank	3 354)	2 725 kg/'000 trap nights
Western Pedro Bank	1 766)	

The comparable catch per unit effort near the Pedro Cays was 2 500 kg/'000 trap nights.

It is difficult to estimate the potential harvest from this area with any precision. Fig. 3 shows that a value close to the maximum could be attained by a fishing intensity equivalent to that exerted by 0.6 canoes/km^2. However, it is not known whether it would be possible to generate such a fishing effort by means of a fleet of fishing vessels utilizing stackable traps or other unconventional techniques which might be developed at some future date.

If it proves to be possible to generate a fishing intensity equivalent to 0.3 canoe/km^2, the theoretical catch from the areas proximal to the edges, or of less than 20 m depth, should be similar to, or greater than, that in the Pedro Cays area; at least 1 450/kg/km^2/year. If the central region of the bank in depths exceeding 30 m be entirely discounted as a source of any production, the remaining area within the 20 m isobath, or within 5 mn of the edge, totals 4 220 km^2 (excluding the 1 000 km^2 presently exploited by the fishermen based at the Pedro Cays). The potential production is therefore at least 6 200 t/year. It is emphasized that this estimate is of the amount attainable using fish traps only in depths of 10-45 m. Additional demersal catches might be taken by trap fishing in deep waters for species at present taken only on hook-and-line.

2.3.5 The handline fisheries for demersal species

There are extremely few data upon which to base an evaluation of the handline fisheries for demersal species. The difficulty lies mostly in the absence of accurate statistics upon which estimates could be based and, particularly, in the poor breakdown of the contributions which different fishing gears make to the total yield in various areas. The best approximation that can be made from the 1968 catch statistics is the total handline catch in the Jamaican nearshore fishery amounted to about 1 000 t, or about 17% of the total catch of neritic species.

Most species which contribute to this catch are concentrated in a narrow zone along the shelf edge on the sill reef, drop-off and deep reef area. Details of species comprising the catches and of the zonation are given by Munro (1974a). Various species of snappers (Lutjanidae) are of major importance, with groupers (Serranidae) and jacks (Carangidae) also contributing substantial parts of the catches. Owing to the concentration of the fishery in this extremely narrow zone along the shelf edge, yields from the fishery are probably best expressed in terms of harvest per km of edge. On this basis, the estimated nearshore catch of about 1 000 t was derived from about 609 km of edge, or an average of about 1 640 kg/km.

It has previously been shown (Munro, 1974a; Kawaguchi, 1971) that stocks of the important snappers, groupers and jacks are very sparse in areas currently exploited by the Jamaican fishery, and unexploited stocks on the margins of Pedro Bank also do not produce catch rates sufficient to support fishing vessels attempting to fish for these species exclusively by handlines or powered reels. It was therefore concluded that it is likely these stocks will be exploited on an opportunistic basis only by vessels fishing primarily using other techniques (most probably using traps). It is probably of significance that virtually no handline fishing is done by fishermen based at the Pedro Cays.

Bearing in mind the limited fishing effort likely to be exerted on these species, the potential harvest from the margins of Pedro Bank could be surmised to lie in the region of 800 kg/km. The circumference of the bank is about 600 km and the likely harvest therefore approaches 500 t/year. Catch rates determined by Munro (1974a) and by Kawaguchi (1971) amounted to about 3.0 kg/line-hour; a harvest of 800 kg/km/year would therefore require at least 270 line-hours of fishing effort/km/year. This could, for example, be achieved by 20 vessels, each exerting an average of 40 line-hours per night for 200 nights of the year. However, the catch per vessel would only average 120 kg/night. This is unlikely to provide a major incentive toward effort in this direction and underlines the belief that this fishery would be conducted only on an opportunistic basis, when conditions of wind and current appeared to be most favourable.

Kawaguchi (1971) and others have shown that, in contrast to Pedro Bank, average catch rates of over 10.0 kg/line-hour can be taken on the edge of the Central American Shelf off Nicaragua, and that similar catch rates can also be achieved quite often at Rosalind Bank and at other banks lying to the southwest of Pedro Bank. These relatively high concentrations of fish stocks have encouraged further investigations in this area, but it remains highly conjectural whether stock densities would be sufficient to sustain the activities of specialized line fishing vessels.

2.3.6 Total potential harvest from Jamaican waters

The total potential harvest from the island shelf and proximal oceanic banks, and from Pedro and Morant Banks is estimated, on a conservative basis, to amount to 15 750-16 950 t/year comprised as follows:

South Jamaica Shelf and adjacent banks (traps, lines and nets)	3 400-4 600 t/year
Northern, Eastern and Western shelves (traps, lines and nets)	3 900 t/year
Pedro Cays trap fishery	1 500 t/year
Morant Cays trap fishery	250 t/year or
Pedro Bank (areas presently unexploited): traps	6 200 t/year
lines	500 t/year
Total:	15 750-16 950

To this must be added landings of oceanic pelagic species (which presently total an estimated 740 t/year) for which the potential harvest is indeterminate. The present total yield from the above-mentioned areas is probably less than 8 000 t/year.

3. POTENTIAL HARVEST OF DEMERSAL AND NERITIC PELAGIC STOCKS FROM THE CARIBBEAN

Gulland (1971) estimated that the potential fish production of the Bahamas region and of the Caribbean Sea respectively amounted to 12-24 kg and 18-40 kg/ha of shelf, and production of demersal fish could respectively provide 2-3 kg/ha/year and 2-8 kg/ha/year of the above-mentioned totals. The bulk (75%-88%) of the catch would be of pelagic species, presumably mostly neritic in habitat.

Moiseev (1971) estimated that production of neritic species in the West Central Atlantic in 1966 averaged 2.9 kg/ha of shelf area, and production in this area could be increased to approximately 8.1 kg/ha/year. However, most species he cites as being possibly underexploited do not occur in the Caribbean and the bulk of the increase is, presumably, expected to come from the Gulf of Mexico and eastern coast of the U.S.A. He also states "there does not appear to be a possibility of including in the fishery in the near future such fishes as coral reef fishes whose numbers are relatively great, but because of habitat and other reasons are unsuitable for fishing". This is clearly a misconception, and might explain some of the disparity between Gulland's estimates of 12-40 kg/ha/year (taking the Caribbean and Bahamas together) and Moiseev's projected maximum for the region of about 8 kg/ha/year.

It is of interest to compare the foregoing estimates with the data given in Table I. The overall Caribbean harvest of demersal and neritic pelagic species is in the region of 4 kg/ha/year; but harvests exceed 7 kg/ha/year in many areas, exceeding 15 kg/ha/year on the coralline shelves of Jamaica, Martinique and St. Lucia and on the non-coralline shelves of Venezuela and Colombia. The detailed data for the Jamaican nearshore fishery (Table II) show that narrow shelves with intensive coral growth, or large expanses of sea-grasses, produce harvests which equal the highest rate (40 kg/ha/year) suggested by Gulland (1971), even when the fish stocks are overexploited with small-meshed traps and nets. Theoretical calculations suggest that harvests of 80 kg/ha/year are feasible if such areas are properly managed. Stevenson and Marshall (1975) give estimates of annual harvests of similar magnitudes for two intensively exploited island shelves in the Indo-Pacific; Mauritius (47 kg/ha) and Ifaluk Atoll (51.4 kg/ha).

If an average harvest of only 12 kg/ha/year be taken from the shelves of the Caribbean Sea and the Bahamas, which total over 66 x 10^6 ha, the total production of demersal and neritic pelagic species will exceed 750 000 t, and an average of 15 kg/ha/year would result in the annual harvest exceeding 1 000 000 t. By way of contrast, the 1973 harvest of all species from the areas considered in this paper amounted to about 330 000 t (FAO, 1974).

Attainment of harvest rates of the magnitude mentioned in the preceding paragraph should not present a major problem in nearshore areas. However, attainment of the necessary fishing intensities in shelf areas which are more than about 25 km offshore presents much greater problems. This is because the major constraints on exploitation of coralline oceanic banks of the Caribbean and the extensive shelf areas of Nicaragua and Honduras are technological and socio-economic. These areas can be exploited only by relatively sophisticated fishing vessels capable of staying at sea for extended periods. Conventional fishing techniques, such as traditional Antillean traps or hook-and-line, have not produced catches sufficient to sustain such vessels; improved techniques such as the use of stackable traps (Munro, 1973) acoustic attractants or artificial baits and improved gear-handling methods must be developed and adopted before exploitation of offshore areas can become an economic reality. The severe regional shortage of skilled engineers and fishing skippers is an additional obstacle.

In nearshore areas, which are intensively fished by small craft, there is every indication that larger mesh sizes for fish traps could result in improved yields. It is perhaps worth emphasizing that, in multispecies fisheries, the conventional economic restraints on overexploitation became operative only long after the largest (and usually the most valuable) fish species, which mature at relatively large sizes, have reached a severe state of biological overfishing, resulting in curtailment of recruitment and a decline (e.g., Fig. 1b) in not only volume, but also in quality and value of the catch.

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BEHAVIOUR AND ECOLOGY OF SCHOOLING GROUPS OF JUVENILE GRUNTS (POMADASYIDAE)

by

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Abstract

Diurnal 'resting schools' of juvenile grunts, primarily Haemulon flavolineatum and H. plumieri, were studied from 1972 to 1976 in shallow water on the northeast coast of St. Croix, U.S.V.I. Juvenile grunts form large inactive multispecies schools in reef areas by day. Repeated censuses over several years reveal that certain parts of the reef, particularly those with large formations of the corals Porites porites and Acropora palmata are traditional schooling areas. Mass-marking experiments using fluorescent pigments blasted into the skin with compressed air show that juvenile grunts will home over long distances to reach a home reef. When the fish reach a size of about 15 cm, the H. plumieri form homotypic schools which roam reef areas, but are no longer associated with particular formations of coral. In contrast, H. flavolineatum remain stationary as schooling adults.

As dusk approaches, grunts stream off their daytime reef areas and swim some distance away (often 200-300 m) into sandy or seagrass (Thalassia) areas to feed. At this time of day there is intense predation on the schools. The routes which are followed are precise, and persist over years. Dawn returns to the reef occur along the same routes. The fish, apparently, use visual cues to detect the routes although other senses might be involved.

Resumen

Desde 1972 hasta 1976 se han estudiado en aguas poco profundas situadas frente a la costa nordeste de St. Croix, Islas Vírgenes, Estados Unidos de América, algunos cardúmenes de roncadores jóvenes, sobre todo Haemulon flavolineatum y H. plumieri, que se mantienen durante el día en estado de reposo. Los roncadores jóvenes forman durante el día, en las zonas de arrecife, grandes cardúmenes inactivos constituidos por diversas especies. Los censos hechos repetidas veces a lo largo de varios años muestran que determinadas parte del arrecife, en especial aquéllas en las que existen grandes formaciones de corales Porites porites y Acropora palmata, constituyen zonas tradicionales de agrupamiento. Experimentos de marcado en masa utilizando pigmentos fluorescentes aplicados a la piel con aire comprimido muestran que los roncadores jóvenes recorren grandes distancias para llegar a la zona de arrecifes donde residen. Cuando los peces alcanzan una talla de unos 15 cm, los de la especie H. plumieri forman cardúmenes homotípocos que se desplazan por las zonas coralíferas, pero ya no están asociados con determinadas formaciones de corales. En cambio, los peces de la especie H. flavolineatum se mantienen estacionarios incluso cuando son adultos.

A medida que se acerca el crepúsculo, los roncadores abandonan las zonas de arrecife donde han permanecido durante el día y recorren cierta distancia (a menudo 200-300 m) para desplazarse a zonas arenosas o cubiertas de plantas marinas (Thalassia), donde se alimentan. En ese momento se produce una intensa depredación de los cardúmenes. Las rutas que siguen son exactas y perduran a lo largo de los años. Al amanecer vuelven al arrecife, siguiendo las mismas rutas.

1. INTRODUCTION

Diurnal multispecies resting schools composed primarily of grunts (Haemulon spp.) were observed in Tague Bay, St. Croix, U.S.V.I., between May 1972 and April 1976. These schools consisting of juvenile individuals (mostly less than 12 cm standard length), are similar to others found throughout the Caribbean and presumably represent a co-evolved predator defence mechanism of the species involved (Ehrlich and Ehrlich, 1973). Heterotypic resting schools are composed of many economically important species (Billings and Munro, 1974). By day they are found in schools near coral formations in reef areas and are generally inactive. As night falls, the fish leave the reef and forage in grass beds or sandy areas through the night, returning at dawn. These nocturnal migrations often occur over long distances (Starck and Davis, 1966; Ogden and Ehrlich, MS.). Similar migrations have been observed in Haemulon sexfasciatum Gill by Hobson (1965, 1968, 1973) in the Gulf of California and in Scarus croicensis Bloch by Ogden and Buckman (1973) on the Caribbean coast of Panama. The movement of large numbers of fish might provide an energy-link between reefs and seagrass beds via organic material carried to the reef and defecated by migrating grunts (Billings and Munro, 1974; Ogden, unpubl.). This report constitutes a part of an on-going study, some details of which have appeared elsewhere (Ogden and Ehrlich, MS.).

2. STUDY AREA AND METHODS

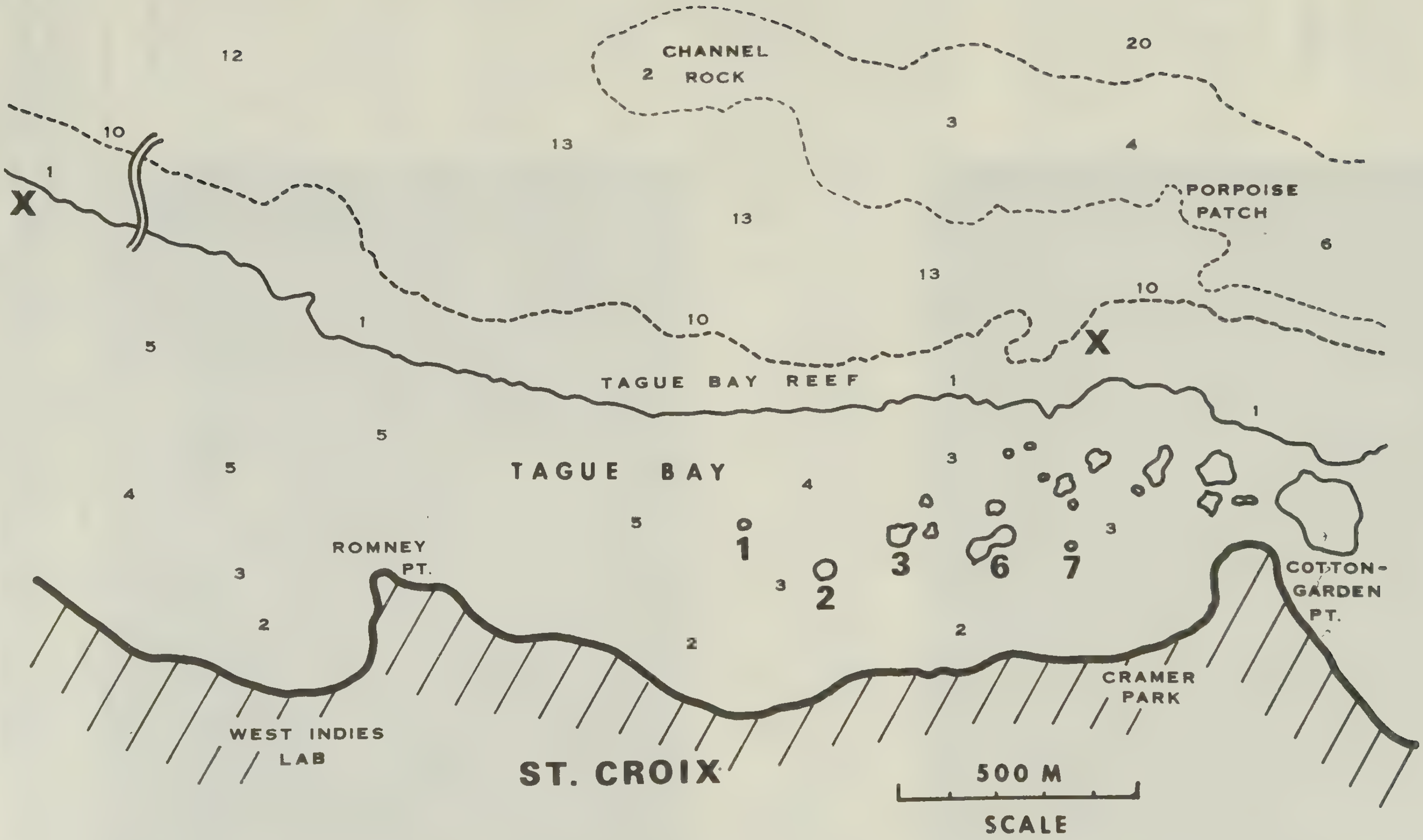
The major study site included 5 patch reefs located in the lagoon behind Tague Bay Reef, just west of Cottongarden Point, St. Croix, U.S.V.I. (Fig. 1). The lagoon floor is covered in most areas with a mixed bed of the seagrasses Thalassia testudinum König and Syringodium filiforme Kutzing. The reefs rise to within 1 m of the surface from about 3-4 m depth. The 5 patch reefs (PR-1, -2, -3, -6, -7) are all roughly circular in shape (with the exception of PR-6), have large populations of the sea urchins Diadema antillarum Phillipi or Tripneustes ventricosus L., and have patches of the corals A. palmata and P. porites growing on the periphery. Two patch reefs (PR-2 and PR-7) had very large populations of grunts and were singled out for intensive study.

Visual censusing was used to record positioning and composition of schools on sketch maps made with compass and meter line. Size estimates were against scaled underwater slates and were checked against size frequency analyses of collected individuals.

The paths taken by various schools leaving PR-2 and PR-7 at dusk or returning at dawn were mapped visually to the reef edge, and extended routes off the reef and into surrounding seagrass beds were traced by weighted markers dropped at dusk while following the fish. These marked routes were then surveyed by day with compass and meter line, and designated by reef number and direction (e.g., PR-2S or PR-7E, Fig. 3).

Once routes were identified, large numbers of fish were relatively easily trapped by placing a V-shaped fence of galvanized ½-in mesh wire, 50 cm high, astride the route. The legs of the "V" were about 3 m long and held in place with reinforcing rod stakes. The point of the "V" led to a large cage approximately 2 x 2 x .6 m made from ½-in mesh wire. The fence and cage were set into place a few metres from the reef, on the route, before the start of the evening migration. As the fish moved off the reef, along the route and into the "V", two divers, positioned at the open ends of the "V", moved in slowly and drove the fish into the cage. With care, large numbers of fish could be trapped using this method. There was no tendency for the fish to go over the fence, and repeated trappings of a particular route were possible before the fish seemed to become slightly wary of the fence and cage.

The marking technique used was introduced by Jackson (1959) and consists of an air blast gun which forces fluorescent (Day-glo) pigment granules into the tissue of the fish with about 100 psi of compressed air. The technique is further described by Phinney et al. (1967) for mass-marking young salmonids. The grunts were held briefly out of water in a wire mesh basket and blasted with pigment from about 40 cm. About 100-200 fish were marked together and immediately replaced in water. Shortly after marking, most of the pigment on the surface of the fish sloughs off, and the remainder is not detectable to the naked eye. Under UV light, however, the pigment granules embedded in the skin are easily seen. The pigment is retained in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ROMNEY
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COTTON-
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WEST INDIES
LAB
ST. CROIX
CRAMER
PARK
500 M
SCALE

Fig. 1 Map of Tague Bay, St. Croix showing Patch Reefs 1, 2, 3, 6 and 7. The two release points for homing experiments are marked with an X. The break in the reef close to the western release point represents 400 m.

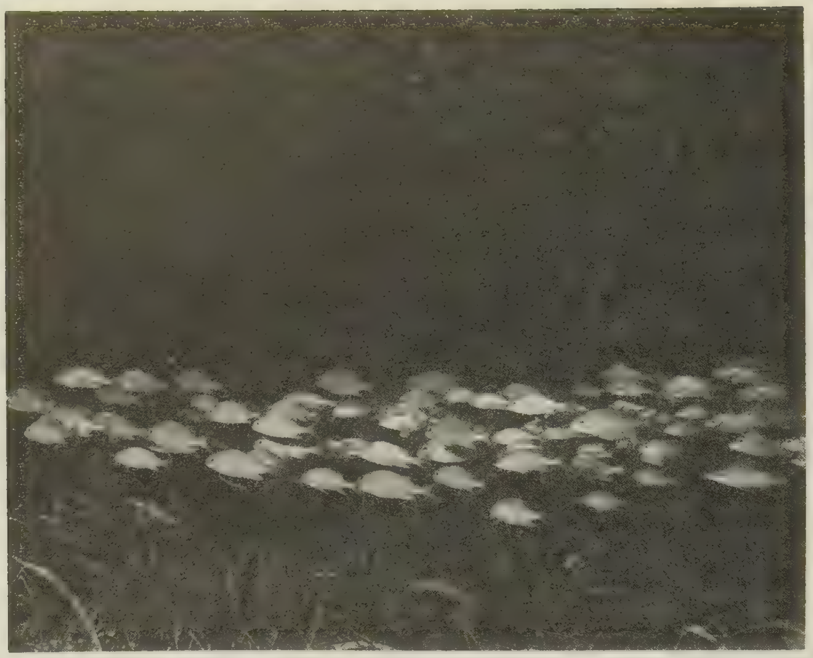

Fig. 2 Column of French and white grunts about 20 m away from Patch Reef 7 during an evening migration

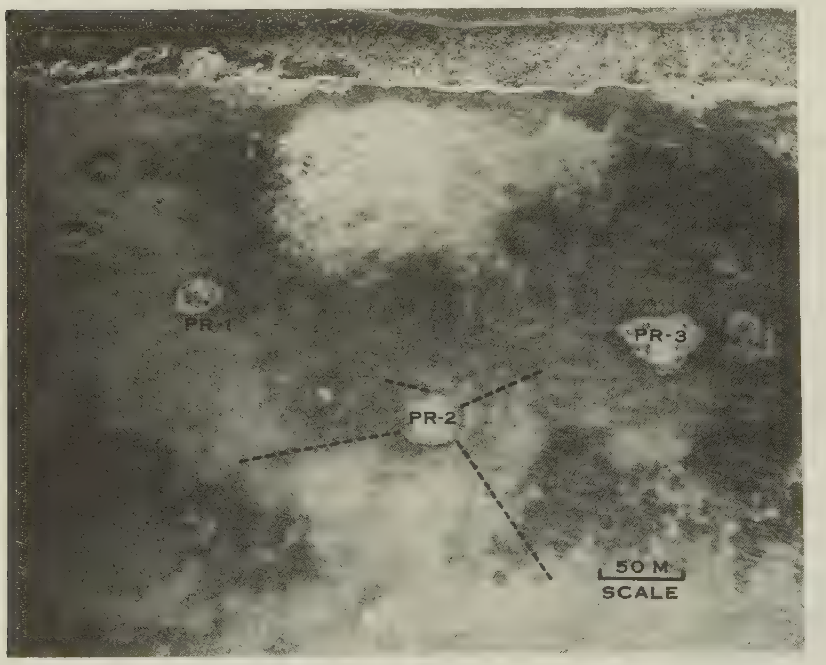

Fig. 3 Aerial photograph of a portion of Tague Bay, St. Croix. Patch Reef 2 appears in the centre with the four routes used by grunts during evening and morning migrations. Fish move much greater distances than indicated. Dark areas are dense seagrass beds, lighter areas consist of sand and seagrass

the skin for at least 2 months and probably much longer. Mortality rates reported by Phinney et al. (1967) in young salmonids were negligible over several months. There was some mortality in grunts immediately following marking, but never more than several fish. The longer term mortality was not examined.

3. RESULTS

On the Tague Bay patch reefs, two Haemulon species; flavolineatum and plumieri, dominated with H. chrysargyreum and H. sciurus often present, but much less abundant. Table I shows the results of censuses made on PR-1, -2, -3, -6 and -7 in August 1973, December 1975 and April 1976. For convenience, the fish were separated into those less than 15 cm standard length and those 15 cm and over. All the reefs have relatively large groups of small H. flavolineatum mixed with small H. plumieri. Large H. flavolineatum are virtually absent from most of the reefs except for PR-2. Each reef has a relatively large group of large (15-25 cm) H. plumieri which roams the reef and the immediately adjacent grass bed. These 'roaming' groups are difficult to approach closely and census. The large numbers of small H. aurolineatum observed on PR-7 in August 1973 are probably a chance occurrence of high recruitment of juveniles to the reef.

Observation of groups of grunts over a long period has given us some insight into the ontogeny of behaviour and the change in daytime schooling patterns with size. Very small (3.5 cm) juvenile grunts, particularly H. flavolineatum and H. plumieri, are especially difficult to identify in the field (Courtenay, 1961) and school together both while in striped juvenile livery and while the adult colour pattern develops, which is from 5 to 12-15 cm in size. The juveniles are usually associated with coral, particularly beds of Porites porites and colonies of Acropora palmata. When the fish are approximately 12-15 cm long, the H. plumieri form roaming groups of up to several hundred fish. They are not associated with any particular coral formation but move about the whole reef. Larger H. plumieri (30 cm) are also found within the lagoon behind Tague Bay Reef. In contrast, larger H. flavolineatum are seen singly in caves, under overhangs, or in the branches of A. palmata, or in similar sites in larger groups. They do not roam, but stay very close to a particular site. Large H. flavolineatum are not common in the lagoon behind Tague Bay Reef. It appears as if they move offshore when reaching a certain size. Groups of large H. flavolineatum are common offshore on Lang Bank at a depth of 20 m.

By day the schools are inactive and H. flavolineatum and H. plumieri were never observed to feed. Very small individuals in the juvenile livery of these two species, as well as small H. chrysargyreum, did feed by day on plankton, taking characteristic head-up poses while they snapped at passing organisms. If disturbed by the observer, the schools became compact and oriented, often diving into the coral to escape.

Table II shows the results of a series of mass-marking experiments designed to test the ability of grunts to recognize a home reef, and a particular location on that reef. In the first series of experiments, 1 592 fish were trapped on the E route of PR-7, given colour marks and transferred to two locations, Tague Transect, 2.8 km west of PR-7 and PR-2E 0.5 km west (Fig. 1). The 904 fish released at Tague Transect on the morning of 27 December 1975 were observed dispersing to the east along the back portion of Tague Bay Reef by the same afternoon and, by the following morning, none were visible in the release area. About 2 percent of the fish released (N=14) were recaptured 3 days later on PR-7E. None of these fish were captured in trappings on PR-7S, indicating that homing had occurred to a particular section of PR-7, most of them (N=41) on PR-7E, but a few on PR-7S. Homing appears to have been directed to a particular area of the reef.

A second series of markings was designed to test the coherence of a particular resting school. A total of 357 fish were trapped on PR-7S and released one day later, after marking at their diurnal schooling site. Two days later, 53 (15 percent) marked fish were captured on the same route. None of these marked fish was ever trapped on PR-7E or on any other route trapped.

A third series of markings was set up to test if fish released outside the barrier reef could home across the reef and into the lagoon. A total of 450 fish were trapped on PR-2W

TABLE I

Summary of Tague Bay Patch Reef Censuses

Haemulon	flavolineatum < 15 cm	flavolineatum 15 cm+	plumieri < 15 cm	plumieri 15 cm+	sciurus	chrysargyreum	aurolineatum	juveniles	Mulloidichthys
PR-1									
17.8.73	515		120	85		1			10
20.12.75	230		90	200	16				
27.4.76	1 100	2	100	150	1				
PR-2									
17.8.73	2 200		175	50					
14.12.75	3 775	300	204	450		100			
27.4.76	1 000	75	300	300					
PR-3									
17.8.73	240		150	100	1	50			30
14.12.75	700	2	600	250	4	75		75	
27.4.76	750		700	220		120			
PR-6									
17.8.73	1 410	5	845	35	1		20	100	3
19.12.75	515	2	425	109	32				
27.4.76	950	20	200	150	25	70			
PR-7									
18.8.73	3 925		825	250	1		1 400		50
14.12.75	2 650		1 650	150				200	
27.4.76	275		125	100					

TABLE II

Summary of mark and release studies on PR-2 and PR-7

Date trapped	Area trapped	No. fish caught[a]	No. and colour recaptured[b]	No. marked	Colour marked[c]	Date released	Area released
26.12.75	PR-7E	904	-	904	Red	27.12.75	Tague Transect
27.12.75	PR-7E	404	-	404	Yellow	28.12.75	PR-2E
29.12.75	PR-7E	284	40 yellow 14 red	230	Yellow	30.12.75	PR-2E
30.12.75	PR-7S	357	10 yellow	347	Orange	31.12.75	PR-7S
31.12.75	PR-7E	51	1 yellow 1 red	-	-	1.1.76	PR-7E
1.1.76	PR-7S	210	53 orange 3 yellow	154	Orange	2.1.76	PR-7S
2.1.76	PR-2E	30	-	30	Orange and blue	3.1.76	PR-2E
3.1.76	PR-2W	81	-	81	Blue	4.1.76	Outside Tague Bay Reef
6.1.76	PR-2W	369	-	369	Blue	7.1.76	Outside Tague Bay Reef
9.1.76	PR-2W	94	12 blue	-	-	10.1.76	PR-2W

a/ Number estimates usually by weight
b/ All recaptured fish held
c/ See text for marking system

and released outside of Tague Bay Reef 0.8 km E (Fig. 1). Three days after the final trapping, 12 fish (3 percent) were trapped which had homed.

The movement of grunts off the reef at dusk and back to the reef at dawn is cued to light level. Observations made in August 1973 showed the evening migration to begin at 18.50 h and to end at about 19.00 h, just as our vision failed. In December, observations made in 1972, 1974 and 1975 showed the migration beginning at about 18.00 h and ending about 18.10 h, at last light. The dawn return occurred between 06.10 and 06.30 h during the December observations. Slight day-to-day variation seemed to occur with cloud cover.

As night falls, the grunt schools in their daytime positions begin to spread out slightly at a uniform distance above the substrate. Individuals are observed to turn on their horizontal axis and catch the fading light, causing a 'flash' which is quite conspicuous. The whole effect is a series of flashes coming from all parts of the loosely aggregated school. This is the only time of day that 'flashing behaviour' is observed, and its function is unknown.

As it gets darker, the actual movement begins. Separate heterotypic schools move or stream along well-defined pathways on the reef surface. The fish swim very close to the surface and a moving stream often divides to bypass an obstacle. The result of the streaming is that several schools may coalesce and continue moving to the reef edge.

Movement continues until large numbers of fish are concentrated on the reef edge. Subgroups of this larger group may have several false starts before rapid movement in columns out into the Thalassia bed occurs at last light (Fig. 2). Once the fish have started moving into the grass bed, they are not easily disturbed by the presence of an observer or by predatory attacks by groupers (Epinephelus spp.), lizardfish (Synodus spp.) and others. Against the background of Thalassia, the fish are very difficult to see at dusk.

The dawn migration is the reverse of the process in the evening with the fish beginning to arrive at about the same light intensity present when they left the reef.

One of the striking features of the dispersal and aggregation of the resting schools is the permanence of the routes. Fish follow these routes long distances out into the surrounding Thalassia bed and return on the same route the following morning. The routes are fixed and unchanging over the short term and reasonably permanent over the long term. Studies on the routes off PR-2 during November-December 1974 showed three routes leading from the reef; one to the north, one to the east and one to the west. In December 1975, the same three routes were present on PR-2, differing from the 1974 routes in subtle detail, and one additional route led to the NW (Fig. 3). Similarly, PR-7 had two major routes in December 1973; one to the east and one to the south. In December 1975, the same two general routes were still present. As shown in Fig. 3, the routes were mapped out a considerable distance from PR-2. The fish move much greater distances than those mapped, but following them in the dark while marking routes proved to be difficult.

4. DISCUSSION

Both daytime resting at highly specific locations and ritualized movements (at least within 50-100 m of the reef at dawn and dusk) occur in heterotypic schools of H. flavolineatum and H. plumieri in Tague Bay, St. Croix. Heterotypic daytime schooling is common in other Caribbean locations, and we see no reason to doubt that detailed investigations would not reveal a similar stereotype of resting place, dispersal and reaggregation behaviour, and choice of routes. Similar behaviour is strongly suspected in H. chrysargyreum, H. sciurus, H. carbonarium and H. aurolineatum, all of which have been observed in heterotypic schools, but which have not been dealt with experimentally here. Castelló (pers. comm.) reports the presence of large heterotypic resting schools of grunts (Haemulon spp.) at Isla Mujeres, Mexico. The schools are known locally as "Los Manchones" or "ink spots", and have been observed as stationary features of the coast for more than 50 y. In one particular reef area (El Garrafón), a very large group of fish is located only 30 m from shore over a sandy bottom 5 m deep, and is protected as a local tourist attraction.

Heterotypic schooling, presumably, has evolved in response to the need to maintain school sizes in communities where the size of individual species populations (and the size classes of individuals within species) is subject to extreme uncertainty. When one species is represented on a reef by only a few individuals in a particular age class, these individuals can gain protection by schooling with other species. For instance, when we herded a group of *H. flavolineatum* and *H. plumieri* toward a trap during the evening migration, we were completely unaware of the presence of a *Mulloidichthys* in a group of 81 grunts (and unable to distinguish the species of grunts) until the fish were placed in an aquarium the following day. So far as we can determine, schooling does not occur at night as the fish forage on *Thalassia* beds.

To the human observer, the routes followed by grunts during their diel migrations have no conspicuous landmarks. The blades of the *Thalassia* wave back and forth in the surge, and the bottom appears uniform and flat. Clearly, however, the route can be sensed by grunts. Small groups of grunts released some distance from a route showed consistent behaviour when encountering a route turning either toward or away from the reef. A net obscuring the details of the bottom provided a clear, if temporary, block to migration. All these obstacles, including fences, observers and so on, are easily bypassed and the route rejoined on the other side (Ogden and Ehrlich, MS.). Almost certainly, all the sensory equipment of the fish plays a role in migration, but probably the most important is vision. Preliminary experiments show that solitary, blinded fish (India ink injected into the eye) do not move but fall to the bottom and lie still. A blinded fish, however, will swim along with normal fish (Ogden, unpubl.).

Due to the difficulty in following grunt groups in the dark and the disruptive effect of lights, we are not certain where the routes lead. The routes leading to the south from PR-2 and PR-7 extend practically to the shoreline. This area is characterized by both lush growths of *Thalassia* and extensive areas of open sand (Fig. 3) either or both of which may have large populations of invertebrates. It is difficult to imagine a reason other than food for such long distance moves, unless the migration puts the fish well away from reef hunting, nocturnal predators.

Long distance homing as evidenced in the mass-marking experiments occurs, but only a relatively small percentage of the fish released home. The migratory habits of grunts probably make them familiar with a relatively wide area surrounding a home reef. It is not known if many of the fish not recaptured at the home reef took up residence on nearby reefs, but certainly none of the PR-7 fish transferred ever showed up on PR-2. The longest recorded distance homed was 2.8 km from Tague Transect. The fish could have used the back of the reef as a line to swim east until they entered familiar territory near PR-7 (Fig. 1), and indeed our observations of immediate dispersal eastward following release strengthens this idea. Fish homing to PR-2 from outside Tague Bay Reef might have brought some other directional sense into play. Within the Bay, the closer the release point was to the home reef, the more fish homed, strengthening the idea of a familiar radius about the home reef.

A number of tagging studies (Bardach, 1958; Beaumariage, 1969; Cummings *et al.*, 1966; Moe, 1966; Randall, 1963; Springer and McErlean, 1962) involving grunts indicate that, over the short term, marked fish are recaptured in the area where they were originally trapped and, in some cases, over a period of many years. Most of these studies involved large fish (15-20 cm + in size). Among juvenile grunts, there is undoubtably quite a lot of moving around before relatively constant adult ranges are set up. McLean and Herrnkind (1971) observed a mass movement of thousands of small grunts (approximately 15 cm), mainly *H. plumieri*, in Bimini. This might indicate that large-scale movements are common in grunts, linked perhaps with ontogeny or with changing conditions in schooling areas.

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ISLAND MASS EFFECTS ON THE DISTRIBUTION OF LARVAE OF TWO PELAGIC FISH SPECIES OFF BARBADOS

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6. REFERENCES

Abstract

Sixteen stations east and west of Barbados, extending to a maximum distance of 26 km offshore, were sampled on five cruises in 1973 using a bongo sampler towed in a step oblique pattern from 60 m depth to surface. Average distribution patterns for the whole year were analysed. Larvae of most pelagic fish were randomly distributed on the station grid; this pattern was seen in the scombrid species Katsuwonus pelamis and in the families Myctophidae, Gonostomatidae and Scombridae. Larvae of the nomeid fish Cubiceps pauciradiatus were significantly more abundant to the west than to the east of Barbados, suggesting concentration of larvae in a standing current system in the lee of the island. Larvae of Bregmaceros atlanticus, a bregmacerotid, were significantly more abundant at stations along the 180 m contour 1.8 km from shore than further offshore. This pattern may be due to upward transport of larvae on the island's slope by internal waves since, unlike most other teleosts, B. atlanticus larvae are most abundant in deep water (depth greater than 50 m).

Resumen

En 1973, durante cinco viajes, se hicieron varios muestreos en 16 puntos situados al este y al oeste de las Barbados, hasta una distancia máxima de 26 km de la costa, utilizando una red "bongo" remolcada en posición oblícua a distintas profundidades, desde 60 m hasta la superficie, y se procedió a analizar la distribución media de formas larvales a lo largo del año. Se halló que, sobre la cuadrícula de los diversos puntos muestreados, las larvas de la mayoría de los peces pelágicos estaban distribuidas al azar; así se observó en la especie Katsuwonus pelamis y en las familias Myctophidae, Gonostomatidae y Scombridae. Las larvas de Cubiceps pauciradiatus (familia Nomeidae) eran mucho más abundantes al oeste que al este de las Barbados, lo que parece indicar una concentración de larvas en un sistema estacionario de corrientes a sotavento de la isla. Las larvas de Bregmaceros atlanticus (familia Bregmacerotidae) resultaron much más abundantes a lo largo de la línea batimétrica de 180 m, a 1,8 km de la costa, que más al largo. Esta distribución puede deberse al desplazamiento de las larvas hacia arriba sobre el talud continental de la isla como consecuencia de olas internas, ya que, a diferencia de la majoría de los demás teleósteos, las larvas de B. atlanticus son más abundantes en aguas profundas (a profundidades majores de 50 m).

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1. INTRODUCTION

Islands have important effects on the oceanic environment, modifying currents (Barkley, 1972; Emery, 1972), vertical water movement (Wunsch, 1972), wave height (Felt and Rabe, 1976), primary productivity (Doty and Oguri, 1956) and zooplankton composition (Sander and Steven, 1973). Effects of islands on the early life history stages of fish are, however, little known. Sale (1970) has suggested that eddy currents in the lee of the Hawaiian Islands can retain larval fish, while Miller (1974) has investigated distribution of larval fish in the near-shore (depth less than 180 m) environment off the Hawaiian Islands, concluding that currents, turbidity and effluents are factors determining larval fish distributions in this area.

The present study is of such a scale as to include the open ocean, an island wake and stations near shore off a small island in an oceanic current system in the western tropical Atlantic. This paper reports on the results of this study as they relate to larvae of several oceanic fish families, and in particular on effects of the island mass on the ecology of the larvae of these families.

Barbados lies 140 km east of St. Vincent (in the Lesser Antilles chain) and 250 km north-northeast of Trinidad. The island's greatest dimensions are 34 km by 22 km, the long axis lying north-south (Fig. 1). Surface water temperatures fluctuate little during the year, from a minimum of about 26.5°C in January-March to a maximum of about 29.0°C in August-September (Lewis _et al._, 1962). Runoff water from the Amazon lowers surface salinities to values less than 34.75‰ in May-August, while during most of the rest of the year, surface salinities are higher than 35.5‰ (Lewis _et al._, 1962). Surface currents off Barbados, probably mainly driven by the trade winds, are essentially constant toward the west-northwest throughout the year (Wust, 1964). Deeper currents can, however, vary greatly in direction, at times even having an easterly component (Warsh _et al._, 1971; Mazeika, 1973). This variable deep current régime may be due to piling up of North Equatorial Current flow against the Lesser Antilles island chain and consequent formation of eddies and countercurrents to the east of this chain (Mazeika, 1973).

2. METHODS AND PROCEDURES

Six transects were established off Barbados, four spread over a sector of 90° downcurrent from the average incident surface current direction of 315° (Wust, 1964) and one each to the southeast and northeast of the island (Fig. 1). Three stations were established on the downcurrent transects, the furthest inshore at the 180 m contour (1.8 km from shore), the others at 12.9 km and 25.7 km from this. Two stations were established on the upcurrent transects, one at the 180 m contour and one 12.9 km from this. Sampling was conducted in February, April, July, September and December, 1973. Different groups of stations were sampled in each month, so the number of samples taken (Fig. 1) is not equal for each station. Fourty-four stations were made during the year.

The 17 m vessel MARTLET, belonging to Bellairs Research Institute of McGill University, was used for occupying stations. Plankton was sampled with a 60 cm bongo sampler fitted with nets of 0.333 mm and 0.505 mm Nitex. The sampler was weighted with a 30 kg weight. Towing speed was 1.3 m/sec (2.5 knots). A step oblique tow was made at each station, with five minutes each at depths of 60 m, 40 m, 25 m and 13 m. Volumes filtered were calculated from readings of a General Oceanics flowmeter in the mouth of the 0.595 mm net. Volume filtered by the 0.333 mm net was taken as equal to that filtered by the 0.505 mm net. Catches were standardized to number per 1 000 m^3.

Samples were fixed and preserved in 10 percent formalin neutralized by saturating with either magnesium carbonate or hexamine (use of hexamine was discontinued early in the study due to its clearing effect on larval fish specimens). Larval fish were removed from plankton samples under a dissecting microscope and preserved in 5 percent neutralized formalin until enumeration. Fish from both 0.505 mm and 0.333 mm nets were counted.

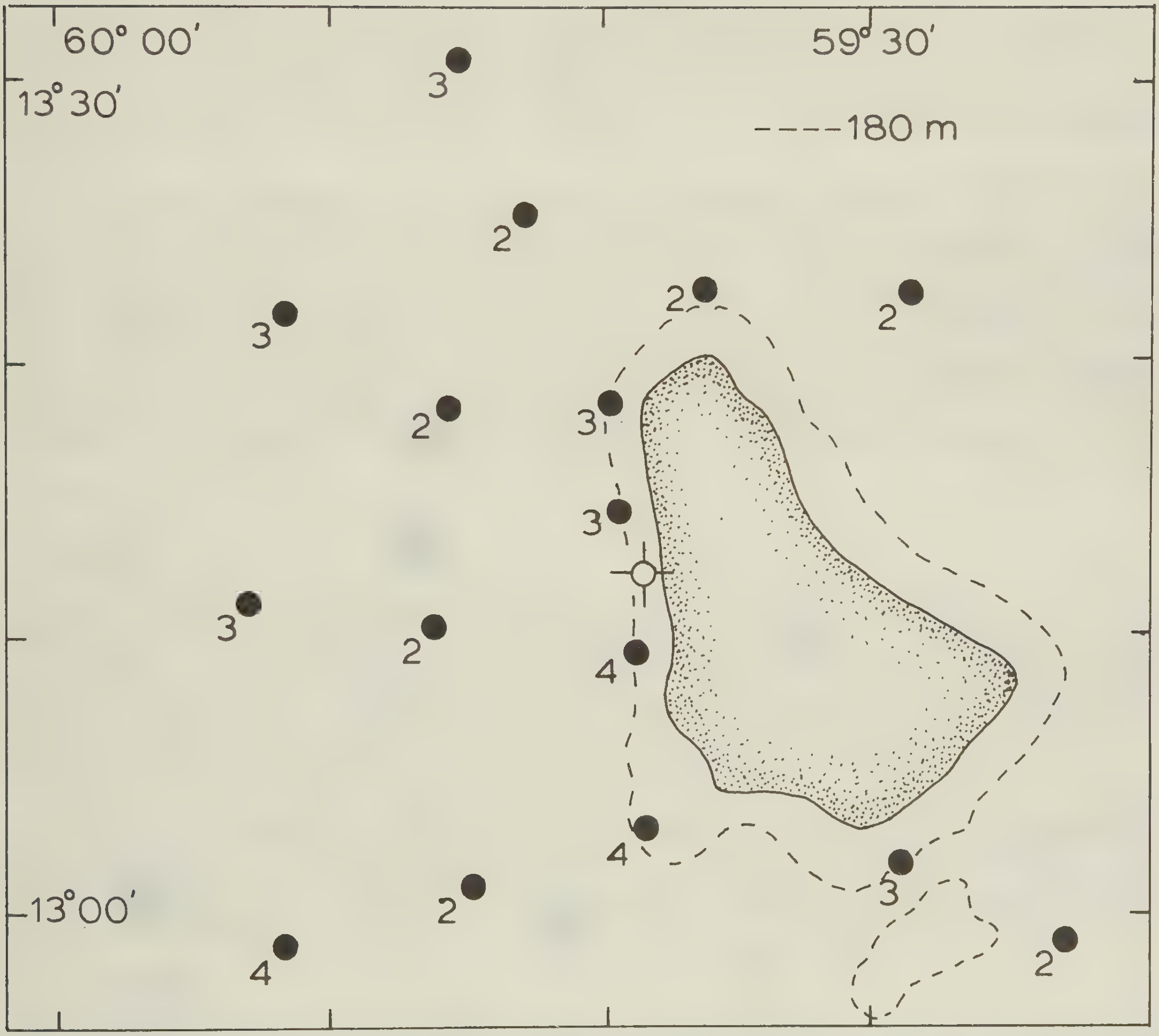
60° 00'
59° 30'
13° 30'
13° 00'
----180 m
3
2
3
2
2
2
3
3
3
2
4
4
2
4
3
2

Fig. 1 Stations sampled off Barbados, 1973. Numbers represent numbers of tows at each station. Dashed line represents 180 m contour

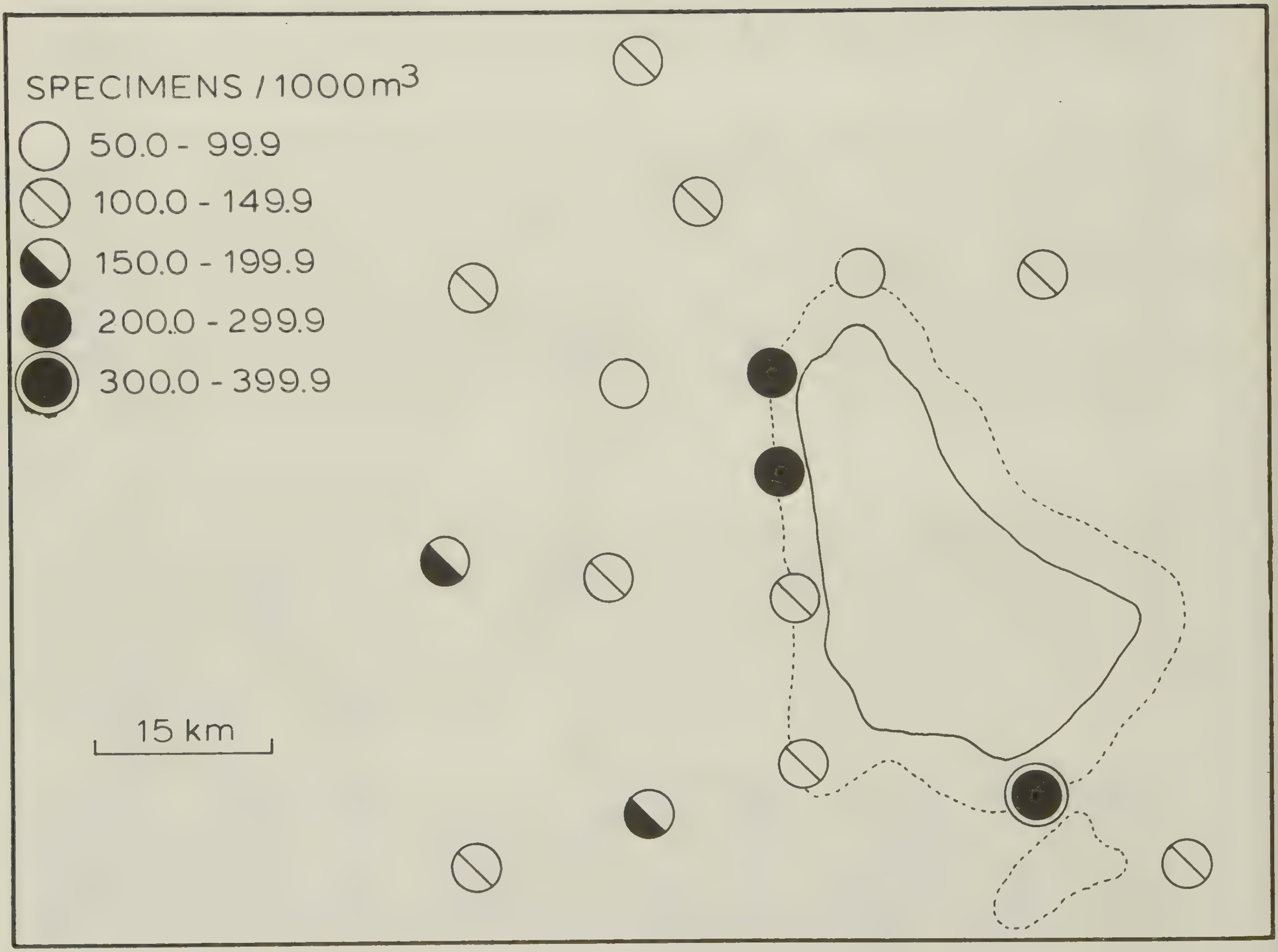
SPECIMENS / 1000 m3
50.0 - 99.9
100.0 - 149.9
150.0 - 199.9
200.0 - 299.9
300.0 - 399.9
15 km

Fig. 2 Mean standardized catches of young Myctophidae. No significant differences between pooled standardized catches of groups of stations with high catches and with low catches

A bathythermograph cast was made to 250 m depth at each station of all cruises except that in February. Temperatures (using Yoshino reversing thermometers) and salinity samples (using Bergen Nautik Nansen bottles) were taken at six depths on every station of all cruises. Salinities were determined by conductance on an inductively coupled salinometer at Bellairs Institute.

For analysis of distribution data, a method was sought which would minimize the problem of patchiness of larval fishes (in this study, patchiness in the data may have been increased by use of a step oblique instead of a smooth oblique tow configuration). In some cases, patchy distributions can be treated statistically by transformation of catch data to a logarithmic base, or by use of a non-normal distribution (such as the negative binomial). In this study, however, a non-parametric test, the Mann-Whitney U test, was chosen for testing the significance of the differences between catch distributions, primarily because the catch distributions for many larval fish groups did not approach the normal, even when transformed logarithmically. Non-parametric methods, which are almost as efficient as parametric methods, require no assumptions about the shape of the distribution investigated for use (Hollander and Wolfe, 1973).

For distribution analysis, results from all five MARTLET cruises off Barbados were pooled for each larval fish group so that an average distribution over the whole year was produced. The following method was used for summarizing distributions over the five sampling cruises. For each group, the mean of all catches during the year (number of specimens per 1 000 m^3) on each station was calculated and is plotted on the distribution maps (Figs. 2-6). The figures were then inspected for distribution patterns and pooled catches from groups of stations with relatively high catches were tested for significance against pooled catches of stations with low catches. Additionally, for each larval fish group, pooled catches of all stations at the 180 m contour and pooled catches of the 4 stations furthest to the east of the island, were tested against pooled catches of all other stations.

3. RESULTS

3.1 Myctophidae

This was the family ranking highest in the larval fish catch off Barbados, with 10 161 specimens (33.7 percent of the total catch of 30 180 young fishes). An average of 145.7 specimens per 1 000 m^3 was caught during this study, with catches on individual stations ranging from 14.7 to 768.4 specimens per 1 000 m^3. Catch rates of larval myctophids over the station grid were at a maximum in July and low in February and December, suggesting year-round spawning with a winter low and summer high (Table I). Larvae of the genera Diaphus, Lampadena, Lampanyctus, Myctophum and Hygophum were taken off Barbados.

Larval myctophids were distributed at random on the station grid off Barbados (Fig. 2). Although stations with relatively high catches were, to some extent, concentrated at the nearshore stations on the 180 m contour and to the west, downcurrent from the island (Fig. 2), there were no significant differences between catches on stations with relatively high and relatively low catches.

3.2 Gonostomatidae

This was the fourth most abundant family in the larval fish catch, with 1 495 specimens accounting for 5.0 percent of the total catch. Average catch rate over the year was 21.4 specimens per 1 000 m^3; catches on individual stations ranged from 2.0 to 280.2 specimens per 1 000 m^3. Catch rates of Gonostomatidae were roughly equal throughout the year except for a very high catch rate in September (Table I). Cyclothone (about 80 percent of the gonostomatid catch) and Vinciguerria (about 15 percent) were the major constituents of the gonostomatid catch.

As with the Myctophidae, gonostomatid larvae were randomly distributed off Barbados (Fig. 3), with no significant differences found between catch rates at groups of stations at which catch rates were relatively high and relatively low. Although not significantly different from catch rates on other stations, relatively high catch rates were found along the 180 m contour and relatively low catches were made offshore downcurrent (west) of Barbados.

TABLE I

Catch rates (number caught/1 000 m^3) of
larvae of major families of oceanic fishes off Barbados 1973

	February	April	July	September	December
Myctophidae	120.0	153.1	205.0	147.9	103.8
Gonostomatidae	10.6	12.3	16.4	77.6	15.6
Scombridae	1.7	6.6	16.3	3.5	3.7
Nomeidae					
Cubiceps pauciradiatus	37.9	23.5	9.7	0.9	15.9
Psenes cyanophrys	0	0.8	0.2	0	0
Bregmacerotidae					
Bregmaceros atlanticus	12.7	0.5	6.6	54.8	100.1
Bregmaceros macclellandii	0.4	0.5	0.7	1.5	1.0

3.3 Scombridae

This family contributed 453 specimens (1.5 percent of the catch) to, and ranked fourteenth overall in, the larval fish catch; average catch rate over the year was 6.5 per 1 000 m^3. Catches on individual stations ranged from 0 to 34.9 specimens per 1 000 m^3. Catch rate was highest in July, lowest in February (Table I), suggesting a summer spawning peak for the family. The scombrid catch was made up primarily of specimens of *Thunnus*, *Katsuwonus pelamis* and, possibly, *Auxis*, with one specimen of *Acanthocybium solandri* and no specimens of *Scomberomorus*.

Scombrid larvae were distributed at random off Barbados, with no significant differences between relatively high catches and relatively low catches on station groups (Fig. 4). As with the myctophids and gonostomatids, stations of relatively high catches were, to some extent, grouped along the 180 m contour. Larvae of *Katsuwonus pelamis* were also distributed at random off Barbados.

3.4 Nomeidae

This family ranked fifth overall in the larval fish catch, with 1 384 specimens (4.6 percent of the total catch). Average catch rate over the year was 19.8 specimens per 1 000 m^3. Individual station catches ranged from 0 to 148.5 per 1 000 m^3.

Two species made up the catch of the Nomeidae, *Psenes cyanophrys* and *Cubiceps pauciradiatus*. Fifteen specimens of *P. cyanophrys* (identified following Legaspi, 1956) were taken, twelve on the April cruise and three on the July cruise. So far as could be determined from these low numbers, larvae were randomly distributed off Barbados.

Cubiceps pauciradiatus (formerly *C. athenae*, recently synonymized with *C. pauciradiatus* by Ahlstrom *et al.*, 1976), with 1 369 specimens, made up 98.9 percent of the nomeid catch. Larvae were identified from fin element counts in large specimens and construction of size series using smaller specimens. Haedrich (1967) gave the following counts for *C. athenae*: DX - XI, I 15 - 16; A II, 14 - 15; these differ sufficiently from counts for *C. gracilis*, the other Atlantic species of *Cubiceps*, to permit specific indentification. Larvae of *C. pauciradiatus* are described and illustrated by Ahlstrom *et al.* (1976).

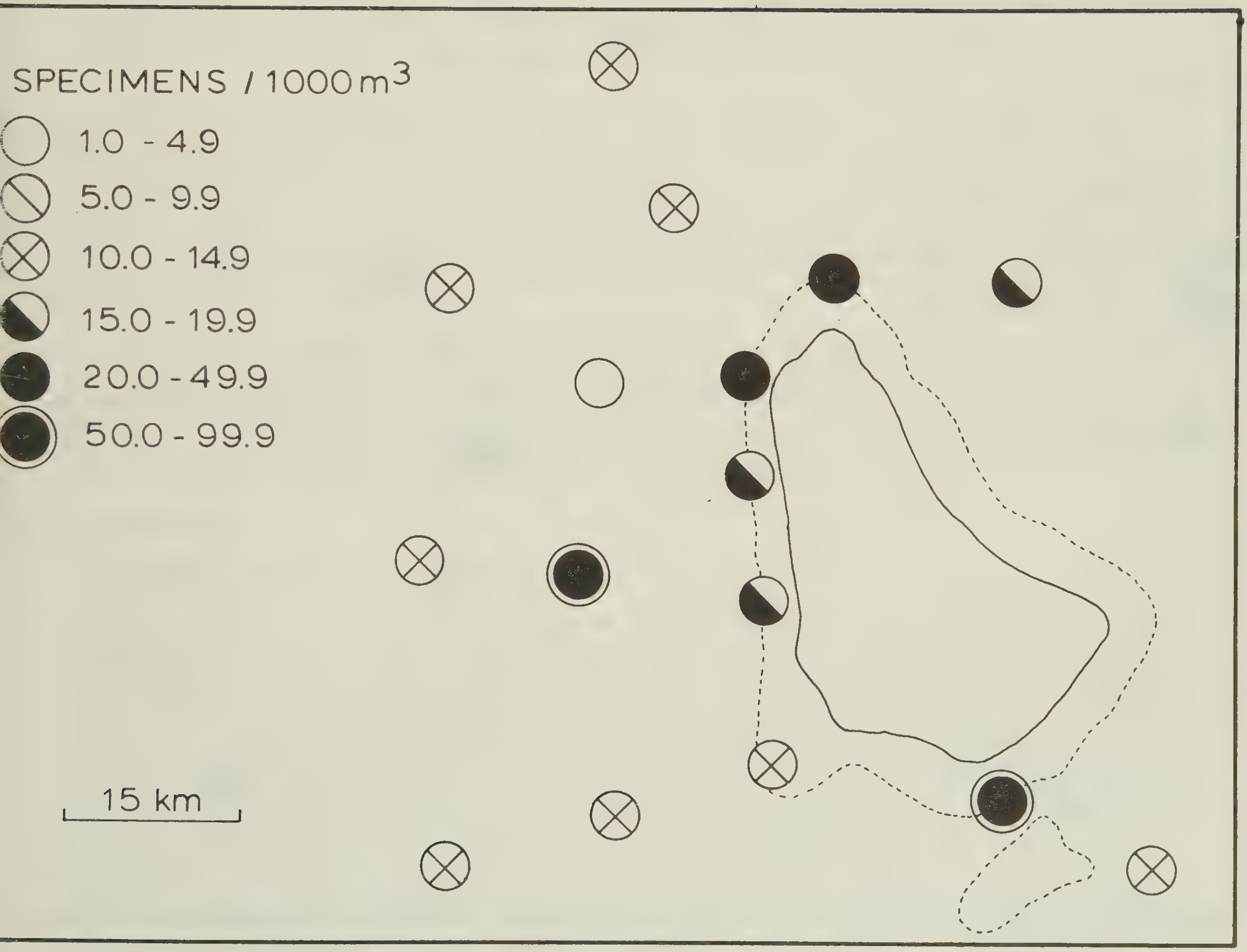
SPECIMENS / 1000 m3
1.0 - 4.9
5.0 - 9.9
10.0 - 14.9
15.0 - 19.9
20.0 - 49.9
50.0 - 99.9
15 km

Fig. 3 Mean standardized catches of young Gonostomatidae over five cruises in 1973. No significant differences between pooled standardized catches of groups of stations with high catches and with low catches

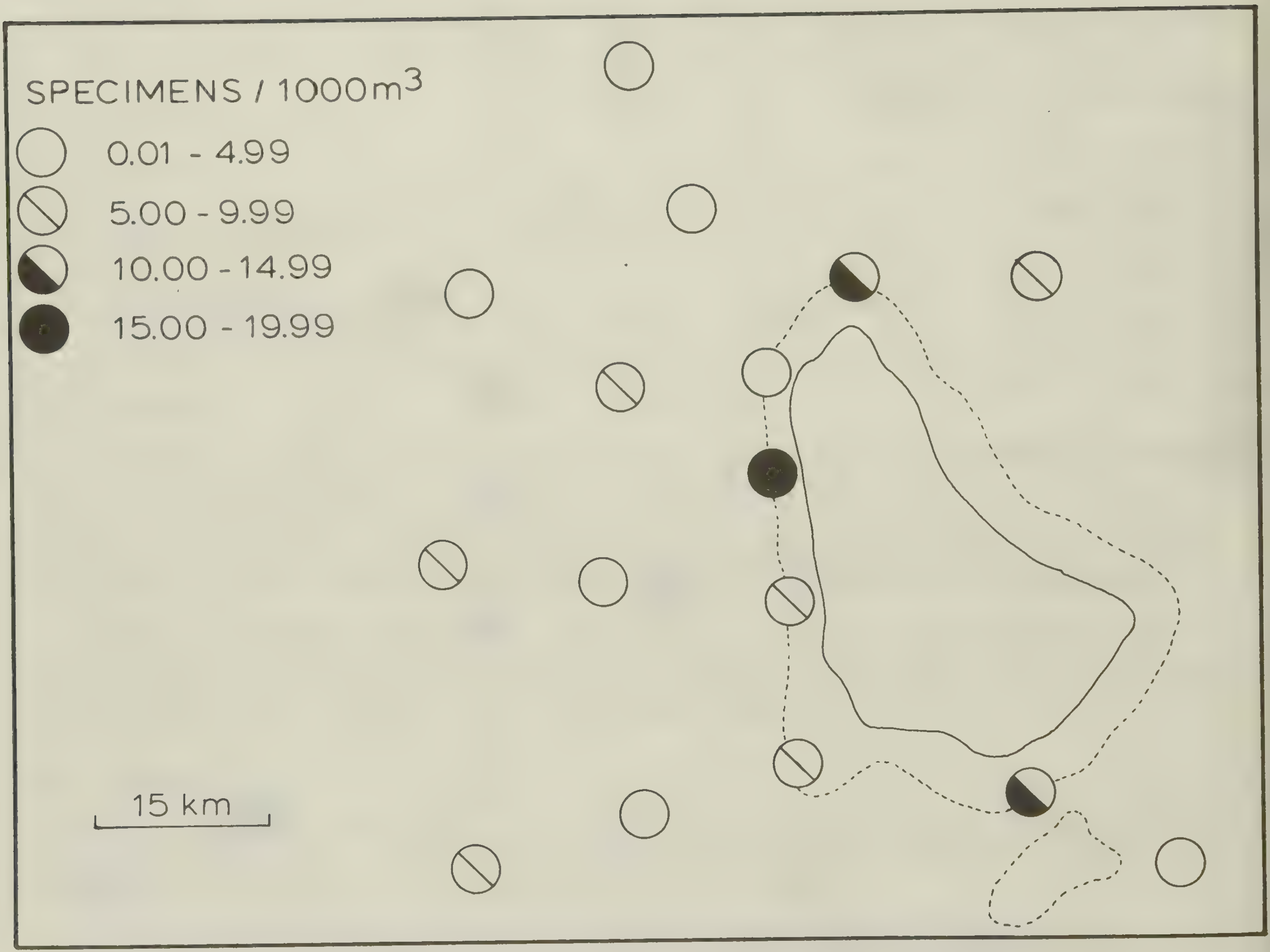
SPECIMENS / 1000m3
0.01 - 4.99
5.00 - 9.99
10.00 - 14.99
15.00 - 19.99
15 km

Fig. 4 Mean standardized catches of young Scombridae over five cruises in 1973. No significant differences between pooled standardized catches of groups of stations with high catches and with low catches

Catch rate of C. pauciradiatus was highest in February and decreased to a minimum in September, suggesting year-round spawning but with a winter maximum and summer-autumn minimum. Catch rates of C. pauciradiatus were higher to the west of Barbados than to the east (Fig.5). Median catch rate for 9 stations to the west of the island was significantly higher (at the 5 percent level) than that on the 7 stations to the southwest and east of the island.

3.5 Bregmacerotidae

Larval bregmacerotids ranked third overall among the families of larval fishes caught off Barbados, with 2 249 specimens (7.5 percent of the total catch). Average catch rate over the year was 32.2 specimens per 1 000 m^3. Individual station catches ranged from 0 to 532.8 specimens per 1 000 m^3.

Two species of the single genus Bregmaceros were identified from the Barbados catch (following d'Ancona and Cavinato, 1965): B. macclellandii, with 51 specimens, made up 2.3 percent of the catch; B. atlanticus, with 2 198 specimens, 97.7 percent.

Catches of B. macclellandii were too small for meaningful statistical tests on distribution on the Barbados station grid. Highest average catches (some 2.5 specimens per 1 000 m^3) were, however, made on stations furthest to the east, the offshore stations on the southeast and northeast transects. B. atlanticus catch rates were higher at stations at the 180 m contour off Barbados than at stations further offshore (Fig. 6). Median catch at the 6 stations at the 180 m contour was significantly higher (5 percent level) than that at the 10 stations further offshore. Very high catch rates (greater than 100/1 000 m^3 were occasionally made on these inshore stations, while the offshore stations usually showed very low (1-4/1 000 m^3) or zero catches.

Catch rates of both species were higher in September and December than in other months in which sampling was conducted (Table I). For B. atlanticus this might not, however, be a true indication of seasonal abundance. Sampling was concentrated inshore and reduced offshore in September and December relative to February, April and July. Since B. atlanticus catch rates were higher on inshore than offshore stations this change in sampling distribution could have accounted for the change in average monthly catch rate.

4. DISCUSSION

4.1 Relative Numbers of Offshore Fish Larvae

The proportions of the catch contributed by larvae of the various families of offshore fishes in this study are intermediate between those of similar studies in offshore and inshore tropical marine areas, confirming the transitional nature of the area studied here. Ahlstrom (1971, 1972), in a large-scale study of the open tropical Pacific, found myctophid larvae to make up some 50 percent of the total young fish catch, gonostomatids 20 percent, scombrids 1.5 percent, nomeids 1 percent and bregmacerotids 2 percent. Guitart Manday (1970), sampling in May 1968 in the Gulf of Cazones off Cuba, found larvae of offshore pelagic fishes to make up some 10 percent of his larval fish catch, with myctophids contributing 2.9 percent, scombrids 0.7 percent and bregmacerotids 0.1 percent; he identified no larval nomeids or gonostomatids in his samples. The proportions of the catch contributed by myctophids and gonostomatids in the present study were less than those of Ahlstrom (1971, 1972) while scombrids made up about the same proportion of the catch in his study as in this. Nomeids and bregmacerotids made up greater percentages of the catch in the present study than in that of Ahlstrom, suggesting that these larvae are indeed more abundant, or more available to plankton sampling gear, off islands than in the open ocean.

Ahlstrom's (1971, 1972) collections of Nomeidae consisted entirely of specimens of Psenes and Cubiceps; this was also the case in the present study. The absence of larval Scomberomorus, which are relatively easy to identify to species level (Wollam, 1970), suggests spawning is limited, or nonexistent, off Barbados. Scomberomorus larvae are taken in significant numbers on the continental shelf in the Gulf of Mexico (Wollam, 1970).

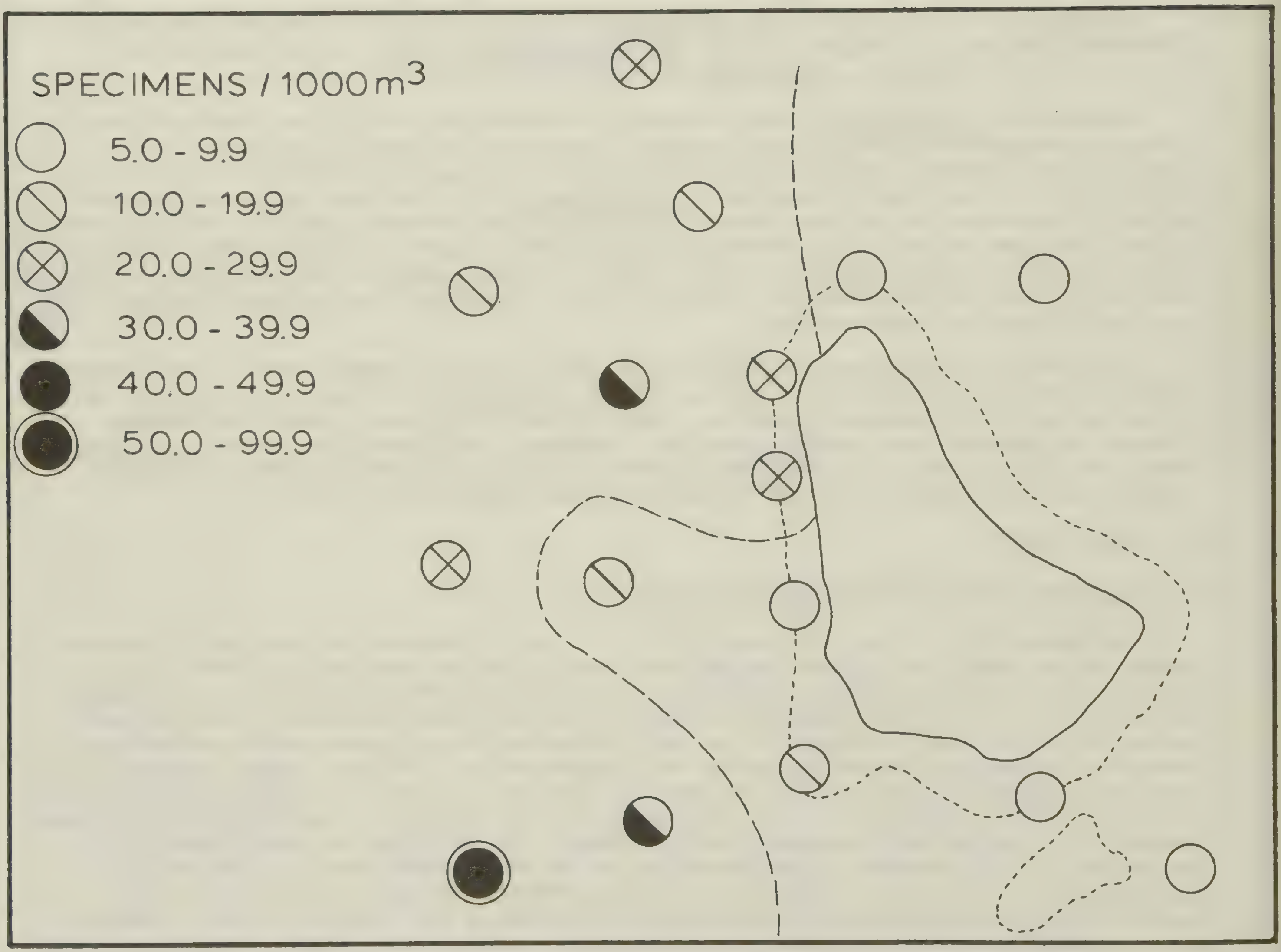
SPECIMENS / 1000 m3
5.0 - 9.9
10.0 - 19.9
20.0 - 29.9
30.0 - 39.9
40.0 - 49.9
50.0 - 99.9

Fig. 5 Mean standardized catches of young Cubiceps pauciradiatus (family Nomeidae) over five cruises in 1973. Pooled standardized catches of 9 stations to left (west, downcurrent) of dashed line significantly higher (5 percent level) than of 7 stations to right (east, upcurrent)

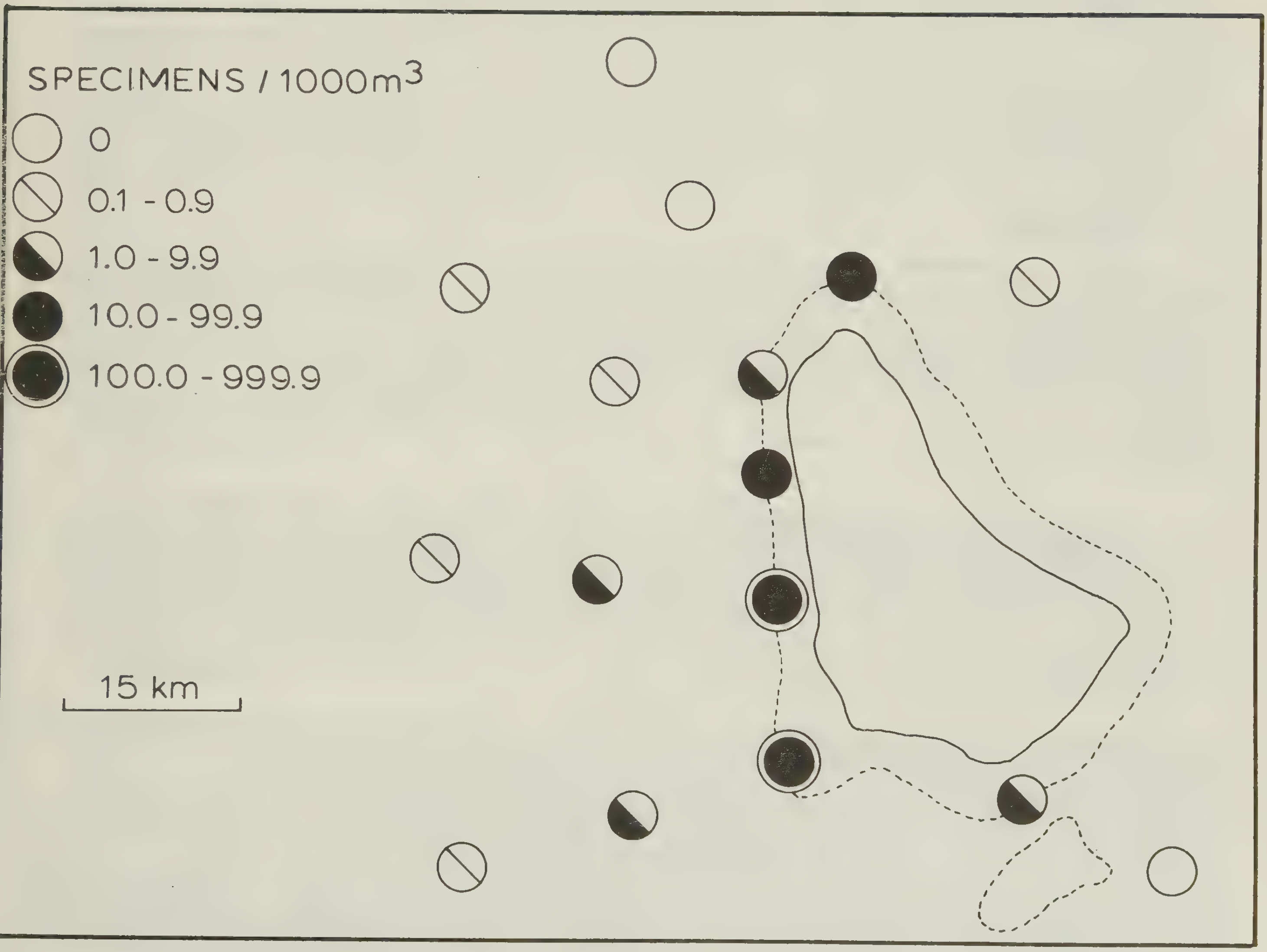
SPECIMENS / 1000m³
0
0.1 - 0.9
1.0 - 9.9
10.0 - 99.9
100.0 - 999.9
15 km

Fig. 6 Mean standardized catches of young Bregmaceros atlanticus family Bregmacerotidae) over five cruises in 1973. Pooled standardized catches of 6 stations at 180 m contour significantly higher (5 percent level) than 10 stations offshore

4.2 Seasonality

Larvae of the five families treated here were caught throughout the year, suggesting some spawning year-round. Seasonal patterns of abundance were noted in several families and species. Myctophid and scombrid larvae were most abundant in summer, least so in winter. Klawe (1960) found larvae of several species of scombrids and of the family as a whole, to be most abundant in the Florida Straits during summer. Larvae of Cubiceps pauciradiatus were most abundant in winter and relatively rare in autumn (September), while gonostomatid larvae were most abundant in autumn.

There is little published information on spawning seasons of pelagic tropical marine fishes, but the above observations are in accord with present knowledge of spwaning patterns in tropical shallow-water fishes. Some spawning appears to occur year-round in Jamaican reef fishes, but most species have periods (of some three months' duration) of increased gonad activity during the year (Munro et al., 1973). The environmental factors triggering spawning seasons off Barbados are not immediately obvious. Day-length and water temperature, the major environmental stimuli for maturation of gonads and spawning in temperate-water fishes, vary little during the year off Barbados. The observed fluctuations in larval abundance accord well, however, with changes in surface salinity, which is low in summer and autumn (June-September) and high in winter and spring (November-March) (Lewis et al., 1962).

4.3 Distribution

Larvae of three families treated here - Myctophidae, Gonostomatidae and Scombridae - were distributed at random off Barbados. In all three, there was a tendency for higher numbers to be taken at stations at the 180 m contour than further offshore. The reason for this is not apparent; a priori one would expect lower catches of larvae of pelagic fishes near shore than further from shore. Similar distributions of offshore fish larvae were reported by Miller (1974), who found larvae of the scombrid Thunnus albacares and the conostomatid Cyclothone more abundant at stations close to shore than at stations further from shore off the Hawaiian Islands. In the present study, however, this trend was not statistically significant and could simply reflect a random occurrence.

C. pauciradiatus larvae occurred in significantly higher numbers over a wide area west than on stations southeast and northeast of the island. Intermediate catches, significantly lower than those in the area of high abundance, were made on stations at the 180 m contour off the southern part of the west coast. This larval distribution suggests spawning is localized in the area west of Barbados, through either concentration of the adult population in this area or localization of spawning to this area in an adult population distributed at random around the island. In either case, it appears that the ecology of C. pauciradiatus is being influenced by the presence of the island.

This larval distribution suggests the presence of a standing current system in the wake of Barbados. Emery (1972) has suggested a von Karman vortex system might exist in the wake of Barbados and this could retain inshore planktonic organisms in the immediate vicinity of the island. Eddies would, however, be shed approximately every 4 days under this current régime (Emery, 1972) and possibly a more stable standing eddy system exists in the island's wake. Brucks (1971) found a large eddy between Barbados and St. Vincent on one of three oceanographic cruises in this area; similar features were not found on the other cruises. Although winds and surface currents are essentially constant from southeast to northwest off Barbados (Wust, 1964), deeper currents may vary greatly in direction (Mazeika, 1973). The hypothetical standing eddy system to the west of Barbados should, therefore, be a relatively shallow feature and larvae of C. pauciradiatus would be expected to have a relatively shallow vertical distribution.

B. atlanticus larvae were caught in significantly greater numbers on stations at the 180 m contour off Barbados than on all other stations. A possible explanation for this distribution is that vertical mixing processes on the island's slope might cause transport of larvae from a randomly-distributed deep population up into the range of the sampling gear. d'Ancona and Cavinato (1965) found larval B. atlanticus to be inhabitants of water layers below the epipelagic zone where larvae of the great majority of fish are found. They stated that *B. atlanticus* larvae were almost never taken with less than 100 m wire out on the sampling gear. Internal wave activity, or other mixing processes on the slope off Barbados, might have caused greater abundance of larval *B. atlanticus* at the depths sampled during this study (maximum 60 m) in the island slope area (i.e., at the 180 m contour) than in areas farther offshore. Wunsch (1972) observed active vertical mixing on the slope off Bermuda and suggested this was due to effects of internal waves or factors associated with the current régime. Sander and Steven (1973) suggested the high nutrient and primary production levels near shore off Barbados are due to the effects of internal waves breaking on the slope. Sampling to greater depths would be necessary to determine whether *B. atlanticus* larvae are in fact distributed at random off the island. If the observed distribution of larval *B. atlanticus* represents their true distribution, spawning of this fish must be concentrated in shallow slope waters around Barbados, through either concentration of the adult population in this area or localization of spawning activity to the area of the upper slope in a randomly distributed adult population.

Hydrographic observations during the sampling trips were not adequate to delineate the current pattern in the wake of the island. Temperature and salinity (and thus density) observations were spaced too far apart vertically to measure the rapid changes occurring within the upper 100 m of the water column. Depths of several isotherms and of the mixed layer, from bathythermograph observations, were plotted over the station grid. Although slopes in these surfaces occurred between stations on some transects, the slopes were not consistent from transect to transect. The most common pattern was a downward slope from the inshore station at the 180 m contour to the next station on the transect, and little slope from this intermediate station to the station farthest offshore, suggesting upward water movement on the island slope. It would appear that, in the dynamic environment of the immediate vicinity of an island, sampling density must be high vertically, horizontally and temporally for collection of hydrographic data suitable for geostrophic current estimates. Direct current observations would also be very desirable for any description of currents in such an environment.

5. ACKNOWLEDGEMENTS

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DISTRIBUCION HORIZONTAL DEL FITOPLANCTON EN EL GOLFO DE CARIACO, VENEZUELA DURANTE 1974

por

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2. MATERIALES Y METODOS
3. RESULTADOS
4. DISCUSION
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Resumen

En 19 estaciones establecidas durante 1974 en el Golfo de Cariaco, visitadas mensualmente, se hicieron estudios para determinar la distribución horizontal del fitoplancton, a profundidad óptica de 50 por ciento de luz incidente. Clorofila *a*, nutrientes, temperatura, salinidad, oxígeno y transparencia fueron determinados paralelamente.

En general el fitoplancton presentó máximos a comienzos del año, dominando diatomeas. De agosto en adelante se notó un descenso con mínimas concentraciones en octubre y noviembre.

En las regiones central y occidental del golfo (1-12), que comprenden la mayor parte del mismo, se observaron máximas en febrero (*Nitzschia seriata*, *Leptocylindrus danicus*, *Cyclotella* sp.), mayo, con el máximo número de organismos (*N. seriata*) y julio (*L. danicus* y *Gonyaulax* sp.) especialmente en las estaciones 11 y 12.

En las estaciones 13-17, que representan la región oriental del golfo, los máximos se observaron en enero (*N. seriata*, *Chaetoceros affinis*, *Ch. decipiens*, *Cylindrotheca closterium*, *L. danicus*, *Eucampia zoodiacus*), en mayo (*N. seriata*) y en julio-agosto cuando se presenta un período de transición observándose abundancia de dinoflagelados (*Gonyaulax* spp.).

La porción oriental extrema del golfo representada por las estaciones 18 y 19 presentó máximos de fitoplancton de marzo a mayo dominando *Cyclotella* spp., *Gonyaulax* sp., *Gyrodinium fisum*, *Rhizosolenia imbricata*, *Pleurosigma* sp. y microflagelados.

Las variaciones en la densidad del fitoplancton están determinadas principalmente por la intensidad de los fenómenos de surgencia en el área.

Abstract

During 1974, 19 stations for studying the horizontal distribution of phytoplankton were established in the Gulf of Cariaco. Samples for phytoplankton counts, chlorophyll *a*, nutrients, salinity, and dissolved oxygen were taken monthly at optical depth of 50 percent of surface incident light; temperature and transparency were measured *in situ* at the same time.

In general, the maximum growth of phytoplankton was observed from January to August, diatoms being the dominant organisms. From September to December a considerable reduction in number of cells/ml was observed, reaching minimum values in October and November.

In the central and western regions of the Gulf (stations 1-12), the maximum values occurred in February (*Nitzschia seriata*, *Leptocylindrus danicus*, *Cyclotella*, sp.), May highest number of organisms per ml (*Nitzschia seriata* and July (*L. danicus* and *Gonyaulax* sp.) mainly in stations 11 and 12.

At stations 13-17, which represented part of the eastern region, maxima were observed during January (*N. seriata*, *Chaetoceros affinis*, *Ch. decipiens*, *Cylindrotheca closterium*, *L. danicus*, *Eucampia zodiacus*), May (*N. seriata*), and July-August, when a transitional period occurred, dinoflagellates being abundant.

In the extreme eastern region (stations 18-19), phytoplankton maximum was observed from March to May, *Cyclotella* spp., *Gonyaulax* sp., *Gyrodinium fissum*, *Rhizosolenia imbricata*, *Pleurosigma* sp. and microflagellates, being the dominant species.

Fluctuations in density of phytoplankton in the gulf area are determined mainly by the intensity of upwelling in the area.

1. INTRODUCCION

El Golfo de Cariaco, con aproximadamente 62 km de largo, 15 km de anchura máxima y 5 km en su comunicación con el mar abierto, está situado en la región nororiental de Venezuela y se caracteriza por presentar procesos de surgencia durante la estación seca, debido a la acción de los vientos alisios.

La descripción geofísica del golfo, ha sido hecha por Roa (1961), y los aspectos hidroquímicos han sido estudiados por Richards (1960), Gade (1961, 1961a; Griffiths y Simpson, 1967; y Benítez, 1974).

Con los trabajos de Curl (1960) y Richards (1960), se inician los estudios sobre la productividad primaria de la zona. Estos fueron continuados por Kato (1962), Hammer (1967) y Mandelli y Reyes (1973). La composición florística del fitoplancton ha sido estudiada por Margalef (1968), quien considera al golfo ubicado dentro de la zona más productiva del área de surgencia del nororiente de Venezuela.

Todos estos trabajos, exceptuando los estudios hidroquímicos, han estado basados en muestreos realizados durante períodos cortos en una o pocas estaciones. El presente estudio se realizó con el fin de tener mayor conocimiento de la distribución del fitoplancton en el golfo y determinar las áreas de mayor productividad del mismo.

2. MATERIALES Y METODOS

Se ubicaron 19 estaciones (Fig. 1), las cuales se visitaron mensualmente y se muestrearon a una profundidad óptica del 50 por ciento de la luz incidente en superficie, determinada en base a mediciones hechas con el disco de Secchi y utilizando las constantes de conversión dadas por Smayda (1966). Esta profundidad fue seleccionada de acuerdo a resultados de estudios previos realizados en la zona por Mandelli y Reyes (1973), que indican una mayor productividad a ese nivel de iluminación.

Se tomaron muestras para estimar el número de células por unidad de volumen, de acuerdo a la técnica descrita por Utermoehl (1958); para nutrientes (fosfatos, nitratos, nitritos y amonio), analizados por métodos espectrofotométricos según Strickland y Parsons (1972); productividad y pigmentos (clorofila a) según Vollenweider (1971); oxígeno disuelto, salinidad, pH y alcalinidad por métodos convencionales. En esta oportunidad se dan a conocer los datos sobre fitoplancton, pigmentos (clorofila a) y nutrientes.

3. RESULTADOS

En las Figs. 2, 3, 4 y 5 se muestran la distribución horizontal de la densidad del fitoplancton, expresada como número de células por ml; clorofila a; nitrógeno inorgánico ($NO_3^- + NO_2^- + NH_3$), y fósforo inorgánico como ortofosfatos, para cuatro meses del año 1974.

En enero (Fig. 2) el máximo número de organismos se encontró hacia el noroeste, asimismo la clorofila a mostró incrementos hacia esta zona, con pequeños aumentos hacia el noroeste. El nitrogeno inorgánico presentó aumentos hacia la región oriental y hacia el occidente, lo cual en ambos casos se debió a un incremento en los niveles de la forma amoniacal. Igualmente los fosfatos mostraron mayores concentraciones hacia la región nororiental del golfo.

En mayo (Fig. 3), se observó el máximo número de organismos, con valores más altos al norte y en la boca del golfo. La distribución de clorofila a, no correspondió exactamente con los valores de densidad de población, ya que sus valores más altos se encontraron hacia el este y el norte. El nitrógeno inorgánico mostró pequeños aumentos hacia la región suroccidental y nororiental y los fosfatos fueron más abundantes hacia el este y norte del golfo.

La Fig. 4 muestra la distribución de los distintos parámetros en el mes de agosto. Se observó mayor cantidad de organismos, así como de clorofila a, hacia la región nororiental.

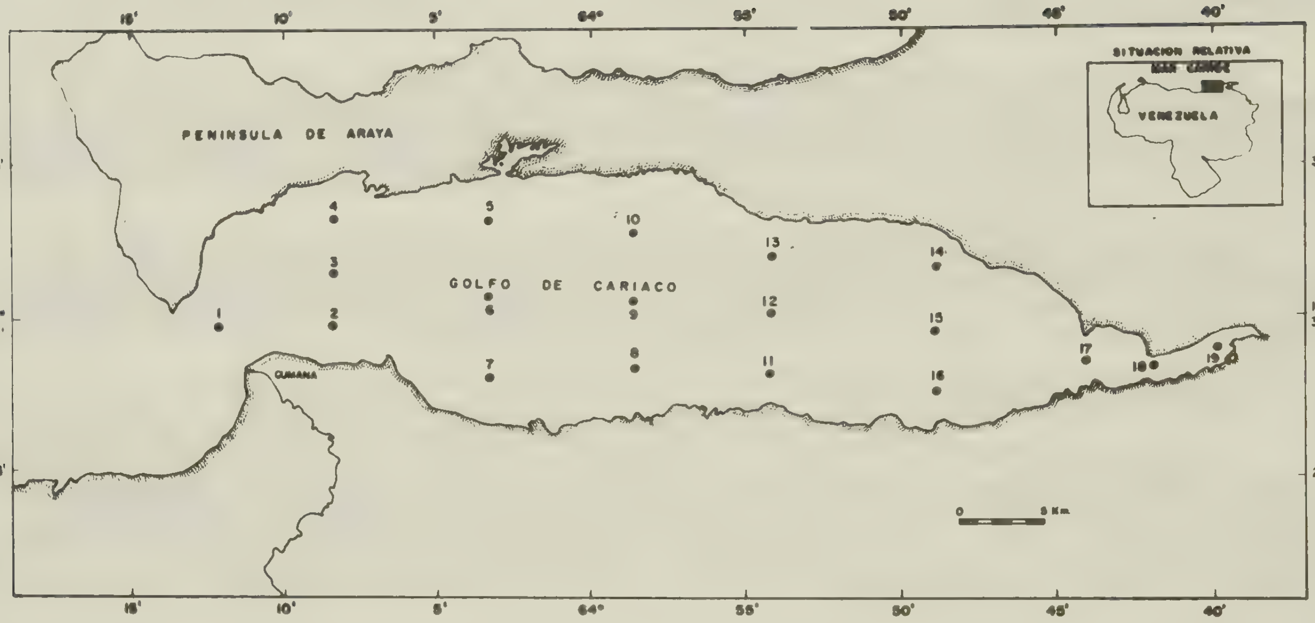
15'
10'
5'
64°
55'
50'
45'
40'
35'
10°
30'
25'
SITUACION RELATIVA
MAR CARIBE
VENEZUELA
PENINSULA DE ARAYA
GOLFO DE CARIACO
CUMANA
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
0
5 Km

Fig. 1 Localización de las estaciones de muestreo y posición relativa del Golfo de Cariaco

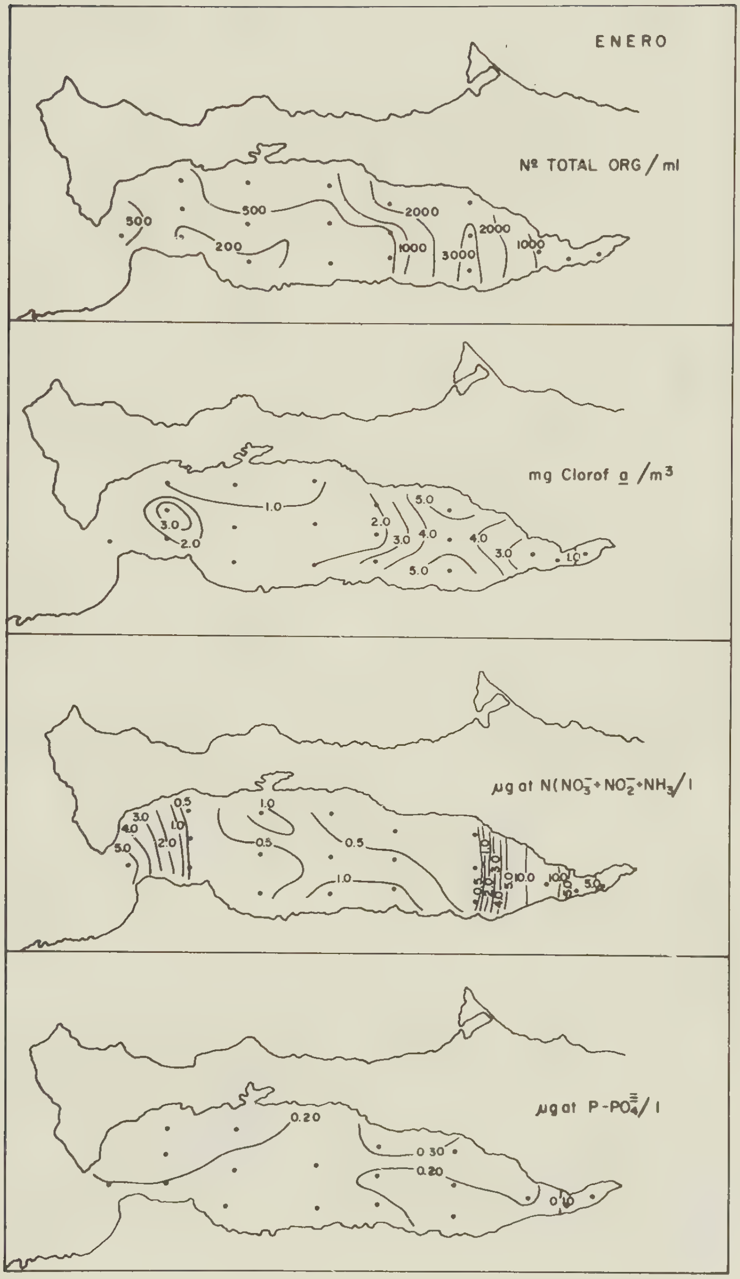
ENERO
Nº TOTAL ORG / ml
500
500
200
2000
1000
3000
2000
1000
mg Clorof a /m³
1.0
3.0
2.0
2.0
3.0
4.0
5.0
4.0
5.0
3.0
1.0
μg at N(NO₃⁻+NO₂⁻+NH₃)/l
0.5
3.0
4.0
1.0
5.0
2.0
1.0
0.5
0.5
1.0
10.0
10.0
5.0
μg at P-PO₄/l
0.20
0.30
0.20
0.10

Fig. 2 Distribución horizontal del fitoplancton, clorofila a y nutrientes, a una profundidad óptica de 50 por ciento de la luz incidente en superficie, para enero 1974

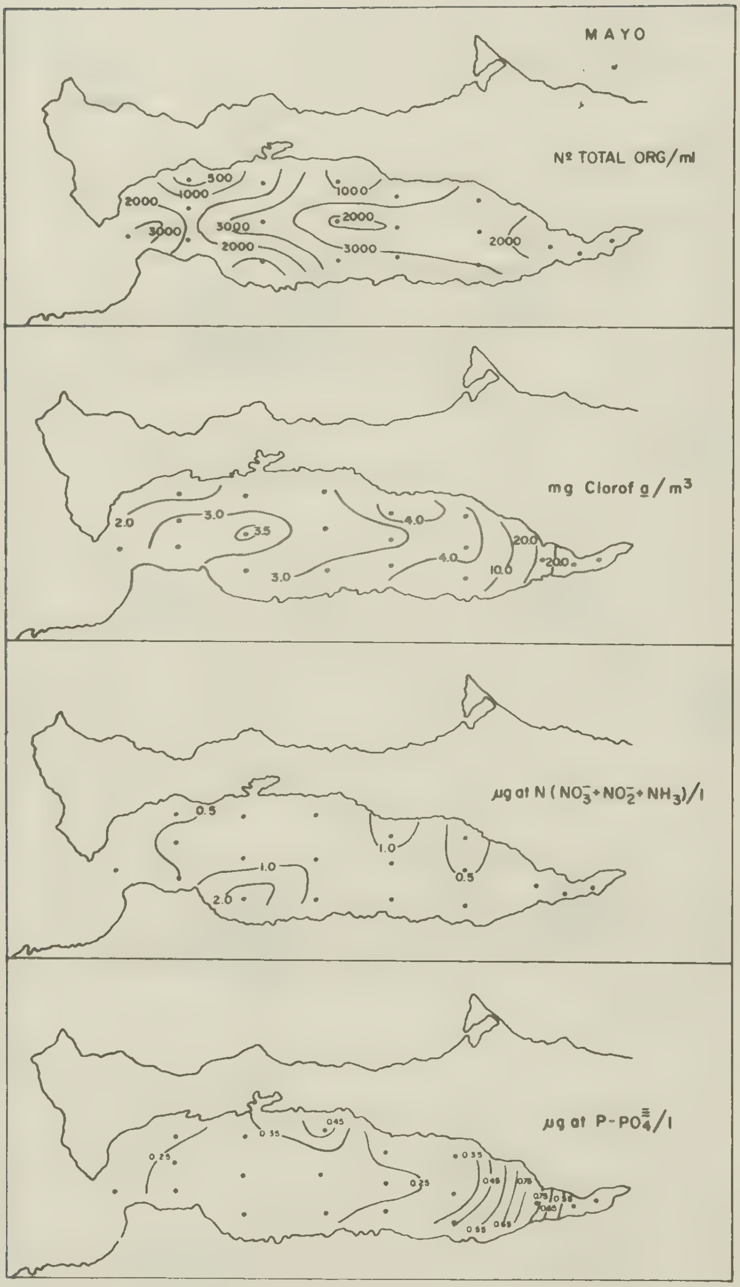
MAYO
Nº TOTAL ORG/ml
500
1000
2000
3000
3000
2000
1000
2000
3000
2000
mg Clorof a / m³
2.0
3.0
3.5
3.0
4.0
4.0
20.0
10.0
20.0
µg at N (NO$_3^-$+NO$_2^-$+NH$_3$)/l
0.5
1.0
2.0
1.0
0.5
µg at P-PO$_4^{\equiv}$/l
0.25
0.35
0.45
0.35
0.25
0.45
0.75
0.75
0.55
0.65
0.55
0.65

Fig. 3 Distribución horizontal del fitoplancton, clorofila a y nutrientes, a una profundidad óptica de 50 por ciento de la luz incidente en superficie, para mayo 1974

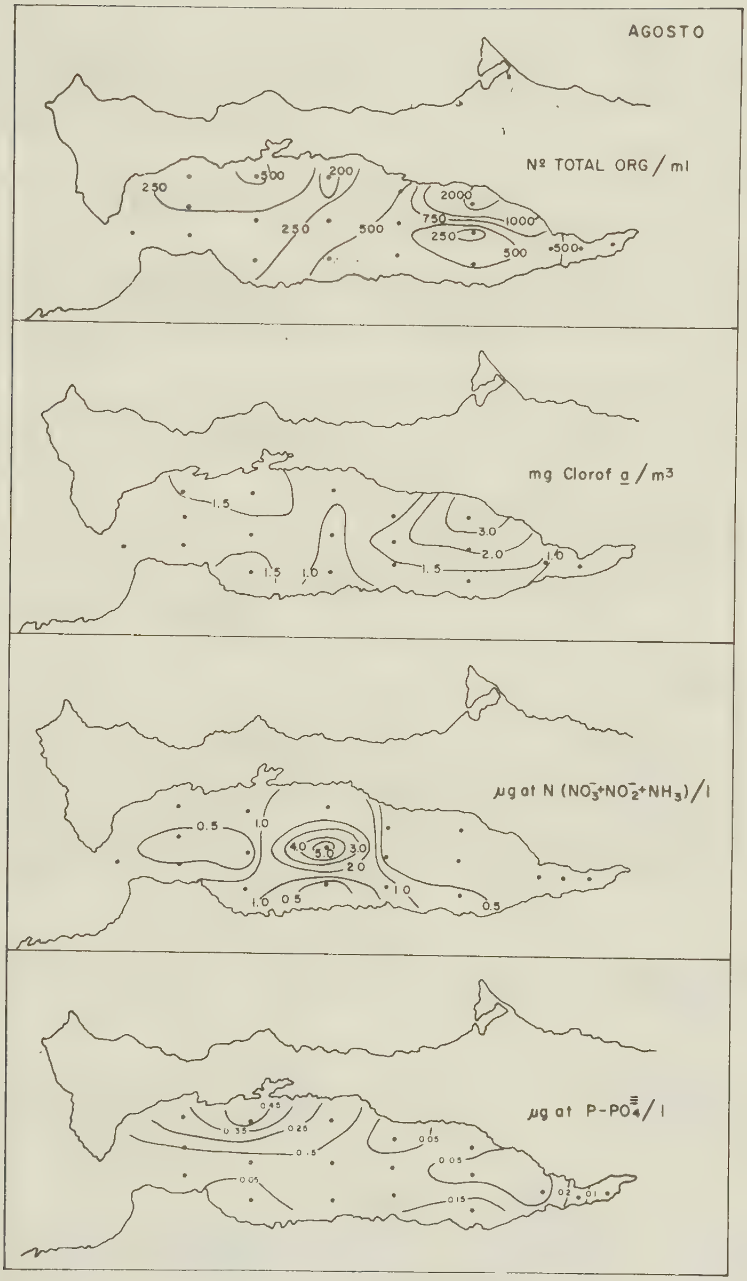
AGOSTO
Nº TOTAL ORG / ml
250
500
200
2000
750
1000
250
250
500
500
500
mg Clorof a / m³
1.5
3.0
2.0
1.0
1.5
1.0
1.5
µg at N (NO₃⁻+NO₂⁻+NH₃)/l
0.5
1.0
4.0
5.0
3.0
2.0
1.0
0.5
1.0
0.5
µg at P-PO₄≡/l
0.45
0.35
0.26
0.5
0.05
0.05
0.05
0.15
0.2
0.1

Fig. 4 Distribución horizontal del fitoplancton, clorofila a y nutrientes, a una profundidad óptica de 50 por ciento de la luz incidente en superficie, para agosto 1974

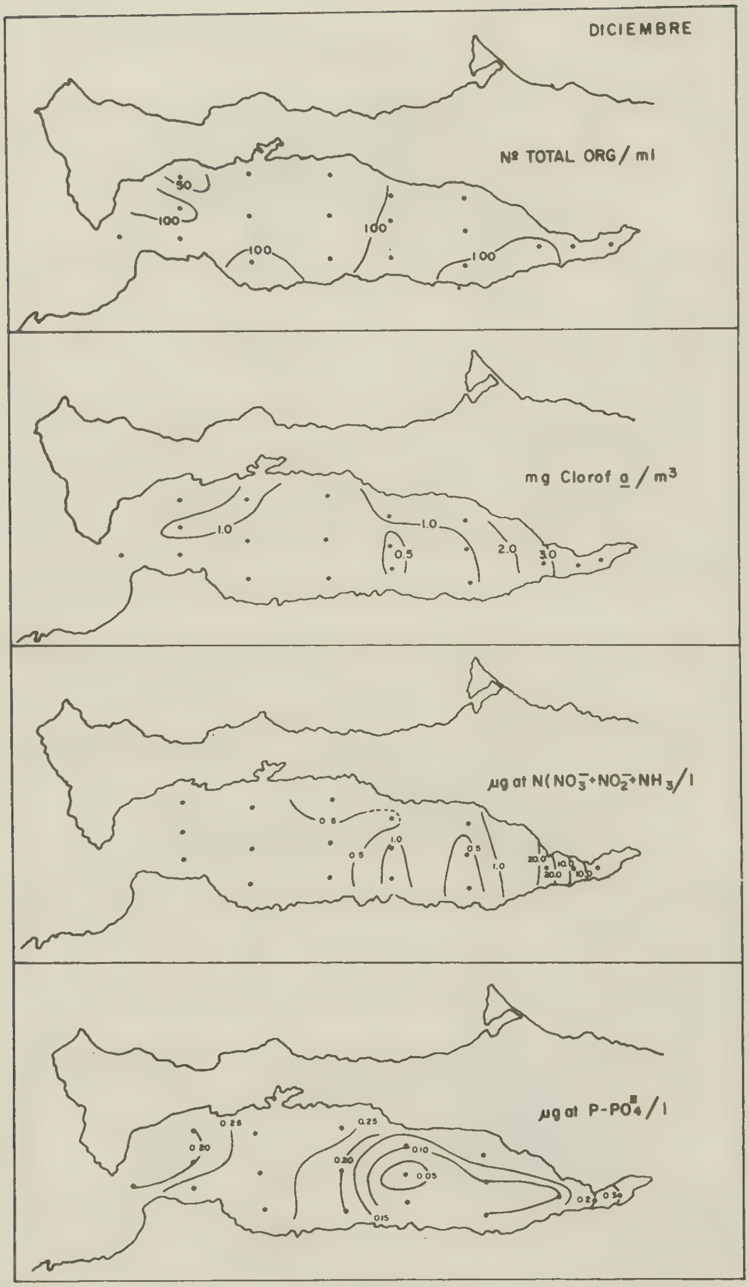
DICIEMBRE
Nº TOTAL ORG / ml
50
100
100
100
100
mg Clorof a / m³
1.0
1.0
0.5
2.0
3.0
µg at N(NO₃⁻+NO₂⁻+NH₃/l
0.5
1.0
0.5
0.5
1.0
20.0
10.0
20.0
10.0
µg at P-PO₄/l
0.25
0.20
0.25
0.10
0.20
0.05
0.15

Fig. 5 Distribución horizontal del fitoplancton, clorofila a y nutrientes, a una profundidad óptica de 50 por ciento de la luz incidente en superficie, para diciembre 1974

El nitrógeno inorgánico mostró valores relativamente altos en todas las estaciones y un valor muy elevado en la región central, debido principalmente a un incremento en los niveles de amoníaco. Los fosfatos presentaron un ligero aumento hacia la región noroccidental.

Para el mes de diciembre (Fig. 5), la densidad de población del fitoplancton es considerablemente baja en toda el área; igualmente se encontraron bajas concentraciones de clorofila *a* y de nutrientes, excepción hecha de las formas de nitrógeno inorgánico, las cuales alcanzaron valores considerables en el saco del golfo.

En la Fig. 6 se muestran las variaciones en el número total de organismos y de la concentración de clorofila *a*, en base a valores promedios de las 19 estaciones muestreadas.

En términos generales, en todas las estaciones, la máxima densidad de organismos se observó durante el primer semestre de 1974, con valores altos en enero, mayo y julio. Luego disminuye hasta alcanzar valores mínimos en octubre y noviembre, iniciándose una tendencia a aumentar en diciembre.

La clorofila *a* presentó aproximadamente las mismas variaciones, sin embargo no se encontró correspondencia entre su concentración en julio y la densidad de organismos.

Las fluctuaciones mensuales en la densidad de organismos en algunas estaciones, escogidas al azar, se muestran en la Fig. 7. Las diatomeas fueron los organismos más importantes siguiendo luego los dinoflagelados y los µ-flagelados. Se observó un comportamiento similar en todas las estaciones, coincidiendo casi perfectamente tanto los máximos como los mínimos en las densidades de organismos.

3.1 Diatomeas

Las diatomeas constituyeron el grupo dominante en el fitoplancton del golfo, salvo en contadas oportunidades, durante los primeros meses del año; en enero y febrero se encontraron las siguientes especies: *Leptocylindrus danicus*, *Nitzschia seriata*, *Eucampia zodiacus* en la mayor parte del golfo, en tanto que en el saco del mismo las especies más importantes fueron: *Achnanthes* sp. *Nitzschia seriata*, *Chaetoceros affinis*, *Ch. decipiens*, *Rhizosolenia imbricata*, *Rh. stolterfothii*. En la estación 19 no se observó una clara dominancia de este grupo.

En marzo, se observaron muchos filamentos de *Chaetoceros* spp. y *L. danicus*, aparentemente parasitados, lo cual estimamos, constituyó la causa de un descenso brusco de la densidad poblacional.

En abril, mayo y junio, nuevamente las diatomeas se hacen dominantes, siendo las especies más representativas *Nitzschia seriata*, *Cyclotella* sp., *Rh. imbricata*, *Cylindrotheca closterium*, en la mayoría de las estaciones, mientras que el saco presenta *Pleurosigma* sp. como especie dominante.

A partir de julio este grupo comienza a perder importancia. En ese mes estuvieron presentes *L. danicus*, *N. seriata* y *C. closterium*; en agosto dejan de ser dominantes, para reaparecer en algunas estaciones orientales en el mes de diciembre (esporas de *Chaetoceros*, *Nitzschia seriata* y *N.* sp.)

3.2 Dinoflagelados

Los dinoflagelados fueron un constituyente importante de la flora en el mes de marzo, cuando *Exuviaella baltica* se presentó en toda el área como organismo dominante, excepción hecha de las estaciones 18 y 19, en las cuales *Gyrodinium fisum* y *Peridinium trochoideum* fueron las especies más abundantes; estas dos estaciones mostraron casi siempre grandes diferencias con las otras, en lo que a la composición florística del fitoplancton se refiere. Así, en la estación 19, se observó dominancia de *Ceratium furca* en enero y de *E. baltica* en junio.

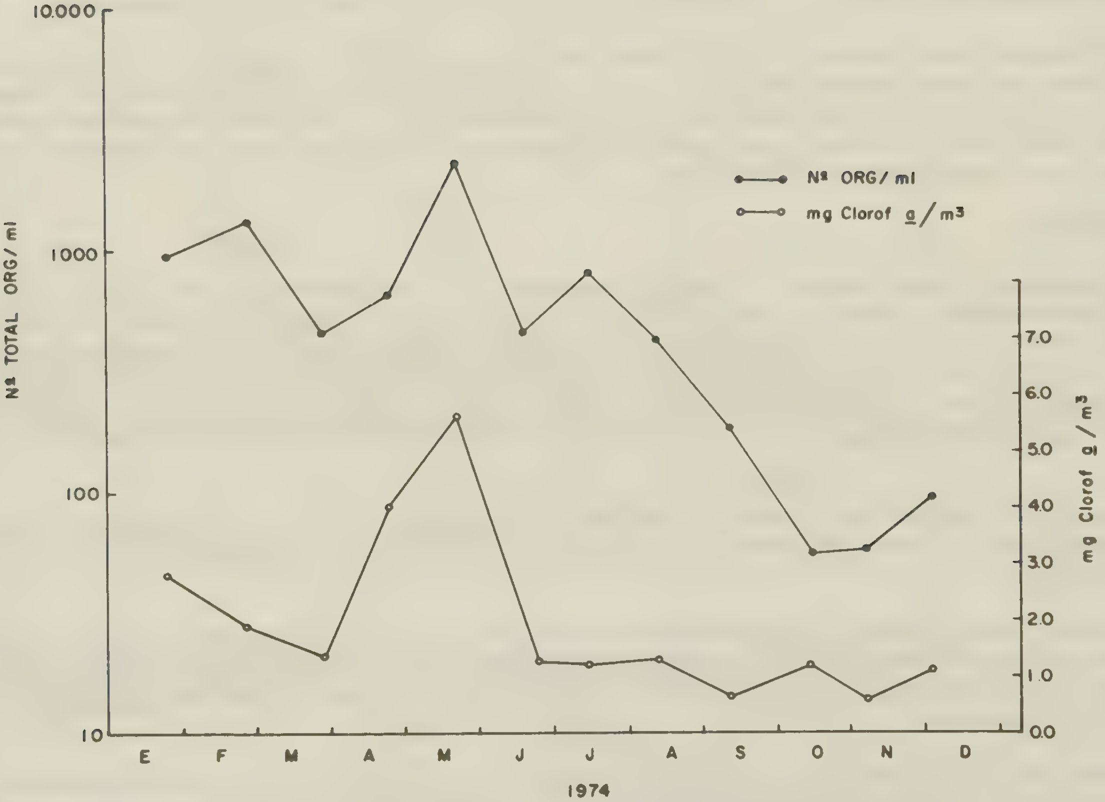

Fig. 6 Fluctuaciones del fitoplancton y concentración de clorofila a, en el Golfo de Cariaco durante 1974

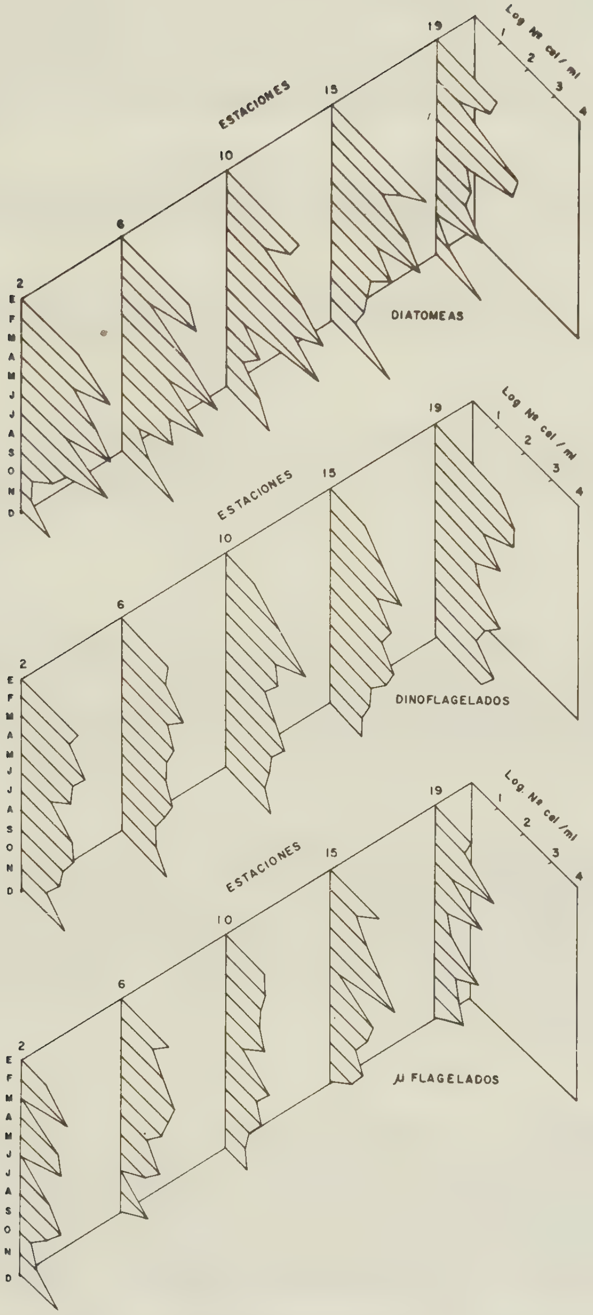

Fig. 7 Fluctuaciones del fitoplancton en las estaciones indicadas, durante el año 1974

A partir de este último mes comienza a cambiar la composición florística del fitoplancton del golfo y en julio se encontraron las especies *Peridinium trochoideum* y *Gymnodinium albulum*, desde la región central hasta la oriental.

En agosto dominaron los dinoflagelados desde la región suroccidental hasta el saco del golfo, con *P. trochoideum*, *G. albulum* y *Gonyaulax polygramma*, como especies más representativas.

De septiembre a noviembre de 1974, disminuyó la densidad de organismos. Las especies dominantes fueron: *G. albulum*, *G. polygramma*, *E. baltica*, *Peridinium minusculum*, *C. furca* y *C. buceros*.

Aparentemente el mes de diciembre se presentó como un período de transición ya que los dinoflagelados solo dominaron desde la región central hacia la suroccidental.

3.3 µ-flagelados

Los µ-flagelados no llegaron a constituir un grupo importante en la composición florística del fitoplancton del golfo, durante el período de estudio. Su abundancia mayor se localizó hacia la región oriental, especialmente en la estación 19, durante los primeros meses del año.

3.4 Meteorología

Los datos de velocidad y dirección del viento, así como los de pluviosidad, para el año de observaciones, se presentan en la Tabla I. Se observa que los vientos alisios tuvieron una intensidad mayor de enero a junio, con máximos en abril y junio. Al mismo tiempo el período de lluvias comenzó en julio, prolongándose hasta noviembre.

3.5 Hidrografía

Las aguas del golfo presentaron pocas variaciones de salinidad y sólo se encontraron diferencias apreciables en las estaciones 17, 18 y 19, durante la estación lluviosa, lo cual podría atribuirse a las descargas del Río Cariaco. La temperatura mostró un rango de variación de 4 a 5°C durante el año, registrándose los valores más bajos durante los meses de surgencia; en cuanto al oxígeno disuelto, no se encontraron mayores variaciones. En la Tabla II, se presentan valores máximos y mínimos de S°/oo, temperatura y oxígeno disuelto, para cinco estaciones representativas.

4. DISCUSION

La aparición de dos máximos de organismos durante la estación seca es un hecho que hemos venido observando con regularidad, a través de los años, en el Golfo de Cariaco, correspondiéndose con el período de surgencias. Herrera y Febres (1975) determinaron que estos eventos intimamente relacionados con la velocidad y dirección de los vientos alisios, se presentan con mayor intensidad durante el invierno y primavera (período o estación seca), principalmente de febrero a abril y ocasionalmente de junio a julio.

De los datos de velocidad del viento, obtenidos para el año 1974 (Tabla I), podemos deducir que los fenómenos de surgencia se produjeron como un proceso casi continuo, a partir de enero, con mayor intensidad en abril y junio, para decaer luego desde julio hasta diciembre, coincidiendo con el período de lluvias. Al aumentar en diciembre la intensidad de los vientos con dirección noreste, comienzan de nuevo a producirse los procesos de surgencia. Estos fenómenos se traducen rápidamente en un aumento de nutrientes disponibles para el fitoplancton y en consecuencia una rápida proliferación de éste, principalmente de las poblaciones de diatomeas, las cuales también se han presentado como organismos dominantes en años anteriores.

TABLA I

Pluviosidad, velocidad y dirección del viento, en el área de Cumaná, durante 1974 (datos proporcionados por la Estación Meteorológica del Instituto Oceanográfico, Universidad de Oriente)

Meses	Pluviosidad mm	Vientos Velocidad m/s	Vientos Dirección
Enero	1,4	4,7	NE
Febrero	0,0	4,9	NE
Marzo	9,6	4,9	NE
Abril	0,0	5,6	ENE
Mayo	1,7	4,5	NE
Junio	6,8	5,1	NE
Julio	20,8	3,9	NE
Agosto	82,7	3,5	ENE
Septiembre	58,2	3,0	SE
Octubre	2,7	3,1	SE
Noviembre	1,8	3,4	ESE
Diciembre	1,3	4,4	E

TABLA II

Valores máximos y mínimos de salinidad, oxígeno disuelto y temperatura, con indicación de las fechas en las cuales se alcanzaron, en cinco estaciones localizadas en el Golfo de Cariaco

	ESTACIONES				
	2	6	10	15	19
Salinidad °/oo					
Máxima	36,8	36,8	36,7	36,8	37,1
Fecha	1 - 74	2 - 74	1 - 74	3 - 74	5 -74
Mínima	36,4	36,3	36,4	36,4	34,9
Fecha	9 - 74	7 - 74	11 - 74	8 - 74	9 - 74
Oxígeno Disuelto ml/l					
Máximo	4,61	5,30	6,02	6,38	4,90
Fecha	2 - 74	3 - 74	3 - 74	1 - 74	3 - 74
Mínimo	3,73	3,85	3,57	3,16	3,06
Fecha	9 - 74	5 - 74	9 - 74	6 - 74	1 -74
Temperatura °C					
Máxima	26,5	26,8	26,4	26,6	26,2
Fecha	9 - 74	9 - 74	11 - 74	11 - 74	11 - 74
Mínima	22,3	22,4	22,6	22,0	22,2
Fecha	4 - 74	4 - 74	2 - 74	4 - 74	3 - 74

La ligera caída en las densidades de las poblaciones fitoplanctónicas, observada en marzo, podría ser atribuida a un descenso en las concentraciones de nutrientes, o bien a efectos del parasitismo observado en esa ocasión, aunque no debe excluirse la posibilidad de un intenso pastoreo por parte del zooplancton, cuya biomasa fue considerablemente alta durante ese período (Urosa, comunicación personal). Sin embargo, es notable el cambio en la composición florística, con predominio en toda el área del dinoflagelado E. baltica, lo cual hace pensar que pudo haberse producido el agotamiento de algún factor o factores por las diatomeas, o en la presencia de algún promotor del desarrollo de este dinoflagelado.

El aumento en la concentración de nutrientes, observado a partir de abril, se reflejó en el crecimiento de la población en ese mes y en el siguiente. La concentración de fosfatos fue bastante elevada en algunas estaciones (1,13 µg-at/l en la estación 2). Así mismo las formas de nitrógeno inorgánico alcanzaron concentraciones altas, sobre todo hacia la región oriental, donde la relación N/P presentó valores altos (8-14); en el resto del golfo los valores obtenidos fueron mucho más bajos, excepto en la estación 5 donde igualmente se alcanzó un valor de N/P=14. Estos valores concuerdan con los obtenidos por Sakshaug et al., 1973, para zonas costeras. Niveles bajos de nitrógeno inorgánico en las aguas superficiales del Golfo de Cariaco, han sido señalados por Benítez (1974), quien destaca la pobreza de los primeros 50 m, al comparar los valores de esta capa de agua, con los obtenidos en estratos más profundos. En mayo tanto las concentraciones de nitrógeno como de fósforo disminuyeron sensiblemente, quizás a causa de rápida utilización por parte del fitoplancton. No obstante se observó cierta correspondencia entre los valores altos de densidad de organismos, clorofila a y nutrientes hacia el norte y nororiente del golfo; en tanto que los altos valores de densidad encontrados en la boca del golfo, no muestran relación positiva con esos parámetros, lo cual nos induce a pensar que se trata de una población senescente, ya que los valores de clorofila a son bastante bajos y se presentaron altas concentraciones de feofitinas. En junio se observó un aumento en la relación N/P, con valores entre 11 y 25, en casi todo el golfo, sin embargo, el aumento de densidad del fitoplancton fue de menores proporciones en el mes de julio, cuando se inicia un descenso en los valores de densidad de población del fitoplancton y de las concentraciones de nutrientes en el área.

El aparente deficit de nutrientes, en especial de formas nitrogenadas en los estratos superiores, puede tener su origen en el rápido aprovechamiento por parte del fitoplancton, quedando posteriormente poblaciones adaptadas a bajas concentraciones de nutrientes, sin que por ello se manifiesten deficiencias fisiológicas, como ha demostrado W.H. Thomas (1970).

Las determinaciones de clorofila a y de sus productos de degradación (feofitinas), mostraron la existencia de poblaciones fisiológicamente jóvenes, sobre todo en los meses de abril y junio, demostrando así que hubo un adecuado abastecimiento de nutrientes, como han observado Morris et al., 1971, para el plancton de regiones tropicales pobres en nitrógeno.

5. CONCLUSIONES

Los estudios realizados sobre el fitoplancton del Golfo de Cariaco, han demostrado la existencia de un ciclo estacional en el desarrollo del mismo. Se observa así un período de proliferación intensa de las comunidades fitoplanctónicas, especialmente de diatomeas, durante los primeros meses del año, cuando por efecto de los vientos alisios se producen fenómenos de surgencia en el área, y luego se observa una declinación progresiva de las comunidades, concurrentemente con un cambio gradual en la composición florística, a partir del mes de julio.

Durante el período de estudio todo el golfo se comportó de manera similar en cuanto a la densidad de población, sus máximos y mínimos.

Las diferencias en la composición florística observadas en algunas estaciones, puede atribuirse a efectos locales, es de hacer notar que estas estaciones están localizadas en áreas someras y pueden además estar influenciadas por aportes de agua dulce.

La concentración de clorofila a, así como de nutrientes, fue mayor hacia la región oriental del golfo.

6. AGRADECIMIENTOS

La autora expresa su gratitud al personal del Instituto Oceanográfico por su valiosa colaboración en la realización de esta investigación, especialmente a los Profesores Taizo Okuda y Gregorio Reyes-Vásquez, por sus recomendaciones y lectura del manuscrito, y a los Sres. Adonay Pernía, Epifanio Hernández y Ramón Vargas, por sus ilustraciones.

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AN OPERATIONAL SURFACE DRIFT MODEL USED FOR STUDYING LARVAL LOBSTER RECRUITMENT AND DISPERSAL[1]

by

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2. THE MODEL
3. INPUT/OUTPUT
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Abstract

A surface drift model which calculates a hypothetical drift path by integrating surface drift velocity in daily increments is used to describe possible drift paths of larval spiny lobsters (Panulirus). Larval spiny lobsters have a long pelagic larval life and are greatly affected by ocean currents. The model provides a fast method of examining possible routes taken by larvae and several examples are shown.

Resumen

Se utiliza un modelo de deriva en superficie que calcula la ruta hipotética de deriva integrando la velocidad de deriva en superficie con los aumentos diarios, para describir las posibles rutas de deriva de las larvas de langosta (Panulirus). Las larvas de langosta tienen una larga vida en estado larval pelágico y son muy afectadas por las corrientes oceánicas. El modelo ofrece un método rápido para examinar las posibles rutas que siguen las larvas. Se dan varios ejemplos.

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[1] Contribution Number 447, National Marine Fisheries Service, Southeast Fisheries Center, Miami, Florida 33149

1. INTRODUCTION

The Miami Laboratory of the Southeast Fisheries Center, National Marine Fisheries Service, U.S. Department of Commerce, has been studying for several years the distribution and abundance of the larval pelagic stages (termed phyllosomes) of spiny lobsters (Palinuridae, Panulirus). The purpose of this study, in part, is to determine the source of recruits for the major fishing grounds in the western North Atlantic Ocean and to determine the dispersal paths of the spawning products of the major stocks of adults. We are not interested in other members of the Palinuridae or members of the Scyllaridae, all of which have similar habits.

The larval stages of the spiny lobster are planktonic and pelagic, spending from six to nine months in the surface layers of the oceans drifting with the currents (Johnson, 1960; Ingle et al., 1963). There are 11 larval stages, termed phyllosome stage I through XI, followed by a puerulus stage (Lewis, 1951). The puerulus stage is a metamorphosed larval lobster which closely resembles the adult and is, essentially, a transparent miniature. This stage settles to the bottom and takes up benthic habits. Phyllosome stages I to XI do not resemble adult lobsters in the least, but are similar to one another and represent molt changes. These phyllosomes are easily identifiable to their respective stage and to their respective genus. Unfortunately, it is currently not possible to identify Atlantic Panulirus phyllosomes to species.

The very long duration of larval drift presents problems in determining the source of recruits and the probable dispersal of spawned products from areas of adult concentrations. The purpose of this paper is to describe a model which, through the use of a computer, generates dispersal and recruitment paths which we believe simulates probable paths taken by drifting larval lobsters.

2. THE MODEL

The model calculates a hypothetical drift path by integrating surface drift velocity in daily increments. The data base grid consists of surface drift velocity averaged by month and by one degree square of latitude and longitude. The model extends from 0° to 35°N latitude and from 50° to 100°W longitude. Land masses and the Pacific Ocean are blocked out in the model's grid.

3. INPUT/OUTPUT

The model inputs up to ten data cards, or card images from tape, containing initial position and times for the drift paths and the number of drift days to be calculated. The output includes a plot (on either a drum paper plotter or a 35 mm filmstrip plotter) of the drift paths and a list of initial and final positions and times. The drift path calculation is stopped at maximum drift days or when the drift path runs into a landmass or into the boundaries of the model.

4. DATA BASE

The data base for the model is a three-dimensional grid (35° latitude by 50° longitude by 12 months) of surface drift velocity. The data were taken from the published pilot charts (Pilot charts of the North Atlantic Ocean. U.S. Naval Oceanographic Publication No. 106. 1969). Each grid point contains either coded velocity information or a code blocking out the particular grid-point as land or the Pacific Ocean. We used the pilot charts rather than generating averages from the original data, in order to get the model operational as soon as possible. A future upgrading of the model will use original data.

5. METHOD

The model determines the earliest month from the input data, then loads from tape the surface drift data base corresponding to that month. The grid-point in which the initial point lies is determined and the change in position due to one day's drift is calculated and plotted. The model then determines if the grid-point has changed or if the month has changed due to the time step in the integration. When the end of the month is reached, the next input data point within the same month is used in the calculations and so on until all possible paths in the month have been calculated and plotted. The model then loads the next month's data base and continues the calculations and plotting. This continues until all the drift paths have been terminated. The data base is handled cyclically, with January following December.

6. DEFICIENCIES

In addition to the problem with the data base, that is the fact that surface velocity was taken from the pilot charts rather than obtained from original data, there are several other deficiencies in the model. The coarseness in the grid is the major deficiency. The model takes into account variations in the currents that are on a space and time scale greater than one month and 100 kilometres. Smaller scale variations are ignored. A second deficiency is that the model uses data averaged over many years, assuming a seasonal cycle to be a steady state. The environment has major year-to-year fluctuations in surface current phenomena, e.g., the timing of the advance of the loop current into the north central Gulf of Mexico, or the wind-driven circulations inshore of the Gulf Stream. A third deficiency is the coarseness of the land mass outline. The land mass is squared off to the boundary of a one degree square. Consequently, the model will calculate a path across the western tip of Cuba or calculate a landfall south of Key Largo, Florida, among other things. While the model cannot be used to predict accurately the path of a drifting object such as a larva or drift bottle, it can be used to study the complexity of possible large-scale surface drift paths. It can be used also to estimate the average drift expected of a large number of drifting items originating at a common point.

7. RESULTS

Our analysis of the data obtained from the model is not yet complete, but certain features are explained here. For our study we determined that there are 22 one degree squares of water around the Bahamas. Within each one degree square we chose 9 equidistant points on 6-day intervals throughout the year. These equidistant points within each one degree square are shown in Fig. 1. The model produced 9 paths shown on a single 35 mm film frame for each day as generated by the computer. These paths were made for dispersal studies (which is making the path follow the direction of the surface current to where a phyllosome would travel) and recruitment studies (which is making the path against the direction of the current to show where a phyllosome would originate). Some of these paths are difficult to discern because of overlapping and limited resolution of the film. The following are examples drawn from these data.

Fig. 2 illustrates the recruitment pattern for the one degree square with coordinates of 27°-28°N; 79°-80°W, on 11 January. Note that paths originate on the north coast of Cuba and end in the subject one degree square. Fig. 3 shows the dispersal pattern on the same day from the same square. Here all the tracks leave the 27°-28°N: 79°-80°W square and travel northward to the end of the chart. These two figures indicate the origin of a phyllosome arriving in this square on 11 January (recruitment path - Fig. 2) or where a phyllosome will go when leaving this square on 11 January (dispersal path - Fig. 3).

Basically, we found that the Bahama banks have three major patterns which are similar within each. Pattern 1: The patterns of the eastern side of the Bahamas all basically exhibit northward dispersals with varying amounts of unusual eddies due to perturbations of the Gulf Stream when the paths are north of the Bahamas. Recruitment patterns all come from

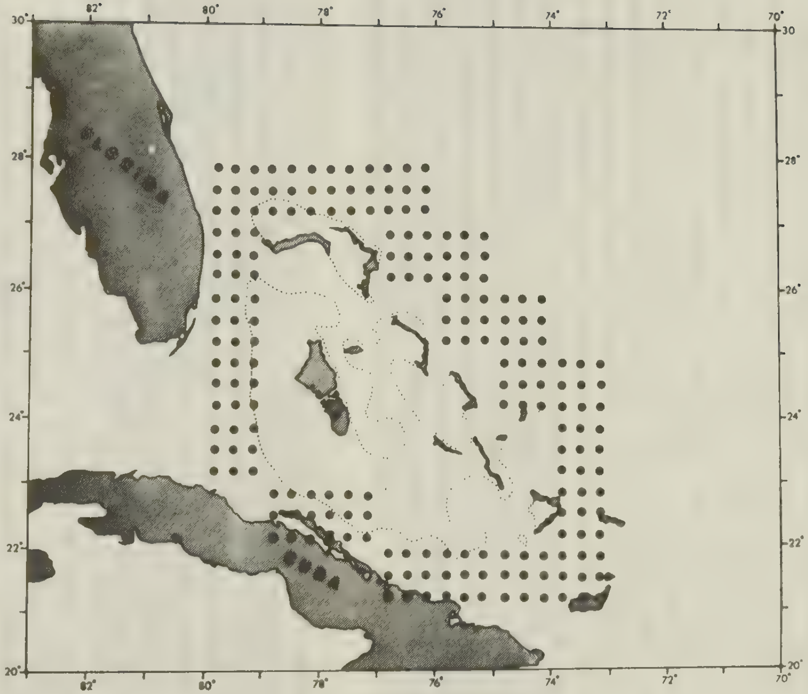
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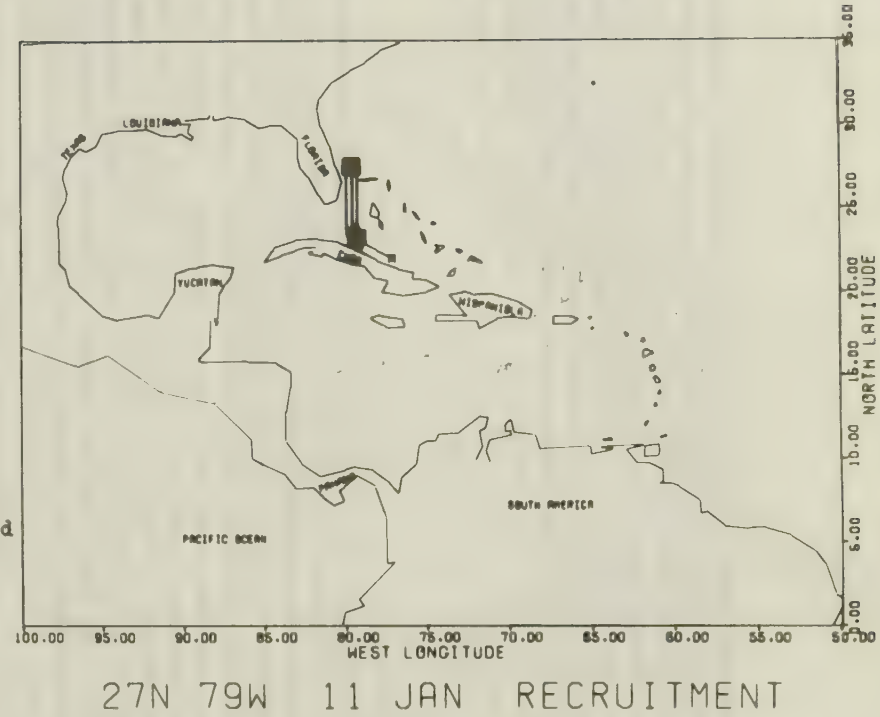
Fig. 1 Chart of the Bahamas showing the location of each equidistant point in the 22 one degree squares studied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27N 79W 11 JAN RECRUITMENT

Fig. 2 Computer generated drift paths for the following one degree square, date and type of path: 27°-28°N:79°-80°W, 11 January, recruitment

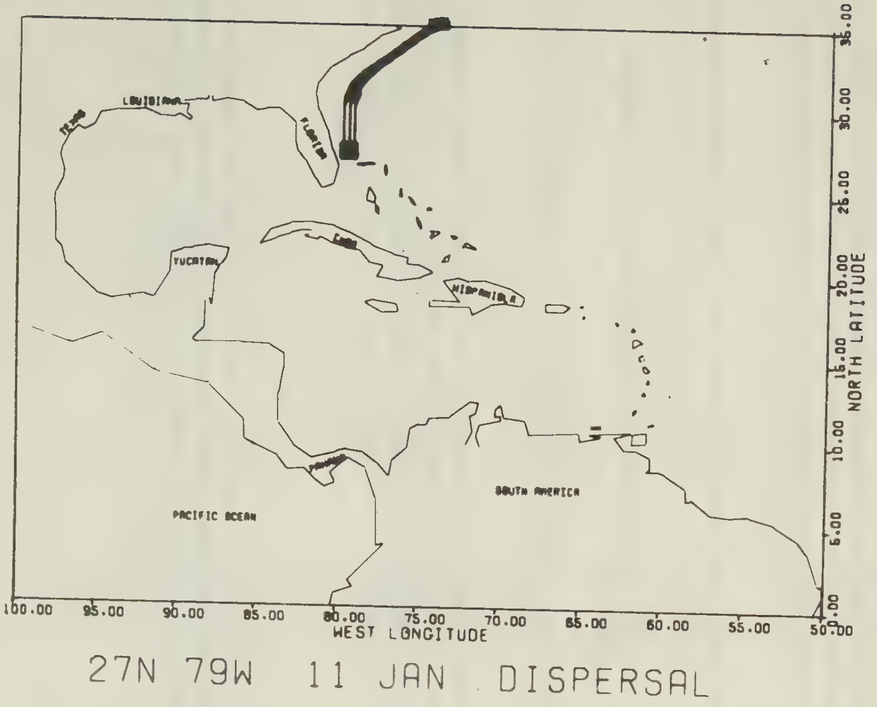
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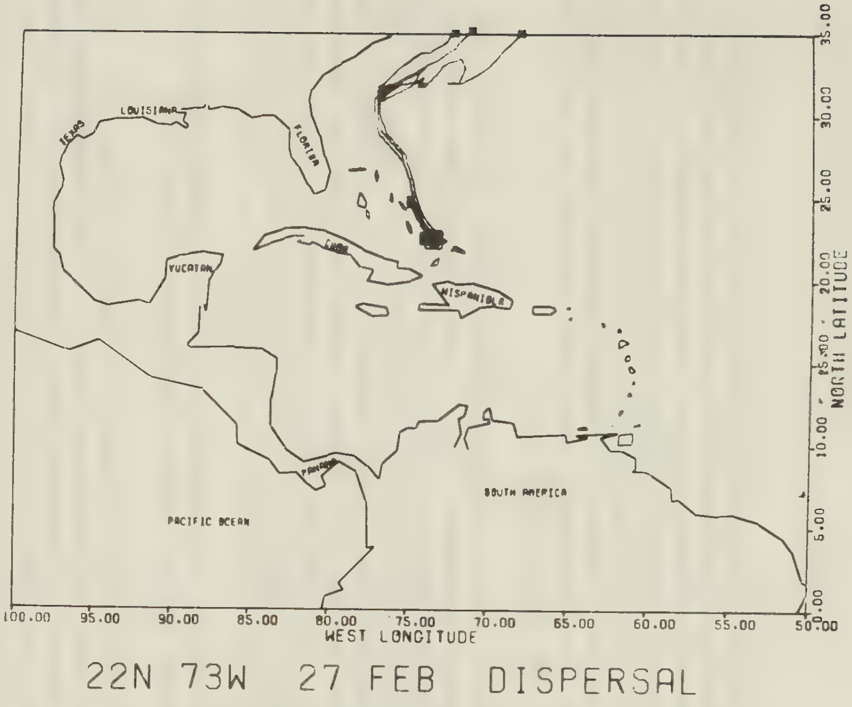
Fig. 3 Computer generated drift paths for the following one degree square, date and type of path: 27°-28°N: 79°-80°W, 11 January, dispersal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22N 73W 27 FEB DISPERSAL

Fig. 4 Computer generated drift paths for the following one degree square, date and type of path: 22°-23°N:73°-74°W, 27 February, dispersal

the eastern edge of the chart; however, at some seasons the currents are deflected southward, with many paths originating from Puerto Rico and the Lesser Antilles. Pattern 2: The patterns of the southern and southwest edge of the Bahamas exhibit little dispersal or recruitment because the distance between the Bahamas and neighbouring Cuba seldom allows a track to traverse the area without it running aground. Pattern 3: The patterns of the western edge of the Bahamas bordering the straits of Florida include dispersal paths which follow the Gulf Stream northward; the recruitment paths move through the Gulf of Mexico, across the Caribbean and through the Lesser Antilles.

Figs. 4 to 14 depict some of these patterns. First are shown the dispersal and recruitment tracks for the eastern Bahamas. Figs. 4 to 7 depict the dispersal from square 22N 73W from 27 February through 11 March at 6-day intervals. On 27 February (Fig. 4) note that three of the paths immediately run aground directly to the west of the point of origin, three more run aground in the vicinity of Cat Island, but the remaining three move northward and get caught in the eddies of the Gulf Stream before reaching the northern boundary of our chart. On 1 March (Fig. 5) a similar pattern developed, but note the wide loop made by one of the paths. On 6 March (Fig. 6) note that the loops made on the previous figure now come south and run aground on Little Bahama Bank as is seen on 11 March (Fig. 7).

Recruitment patterns for the western edge of the Bahamas generally show direct movement from the eastern boundary of our chart to the Bahamas (Fig. 8).

For the southern edge of the Bahamas (the area bordering with Cuba) there is virtually no dispersal until we reach the southeast corner of the Grand Bahama Bank, (Fig. 9, for 16 April). Note the degree of dispersal due to pertubations of the Gulf Stream. Recruitment to this area comes from the east as shown in Figs. 10 and 11. Note the origin at Puerto Rico and the traversing of the Lesser Antilles. For the western border of the Bahamas northward dispersal into the Gulf Stream and associated swirling and eddying of the paths is depicted (Fig. 12). Recruitment paths from this side are quite interesting (Figs. 13 and 14). Here we see origins on the coast of Cuba, Honduras and various islands in the Lesser Antilles.

From studying all the photographs of these patterns (a total of 1 584) we have reached the following preliminary conclusions:

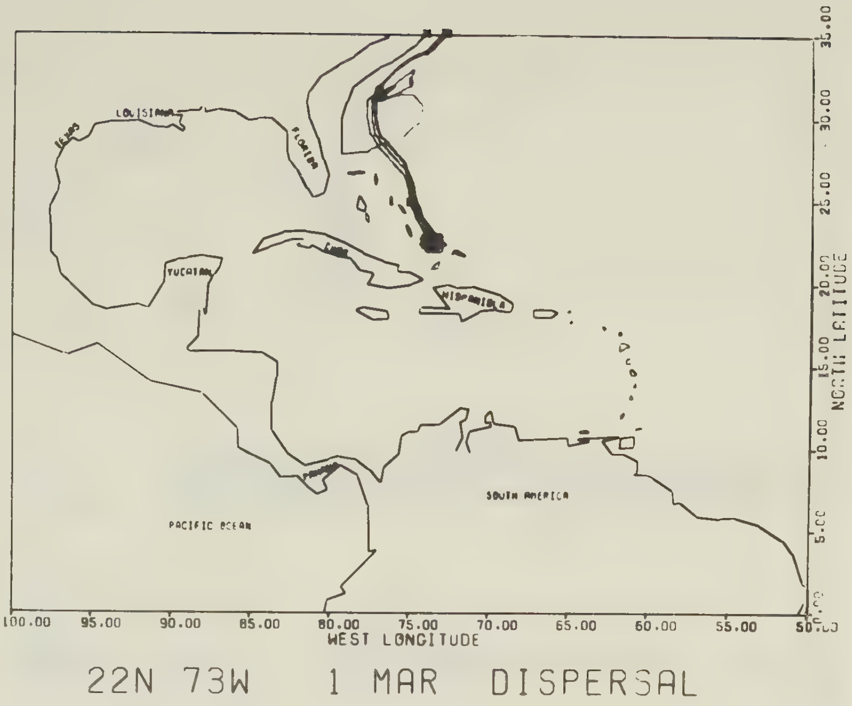
(1) A significant portion of Bahamian recruits must come from upstream in the current system, principally from the Lesser Antilles.

(2) Larvae produced by the Bahamian stocks are swept northward by the currents and a significant portion is probably lost in the North Atlantic drift.

(3) There is no firm evidence that larvae produced by Bahamian adults would ever return to the Bahamas as recruits. However, we plan to expand our areas for plotting purposes to calculate the likelihood of a path leaving the Bahamas and returning in 6 to 9 months. Our present data indicate that, for the periods involved, most recruits originate in the Lesser Antilles.

8. CONCLUSIONS

The surface drift model allows one quickly and easily to gain some insight into surface current paths which affect drifting organisms and thus make important hypotheses on biological consequences. We feel that the model can give reliable indications of dispersal and recruitment paths within the limits considered, thus providing us with a valuable tool for research into drift problems.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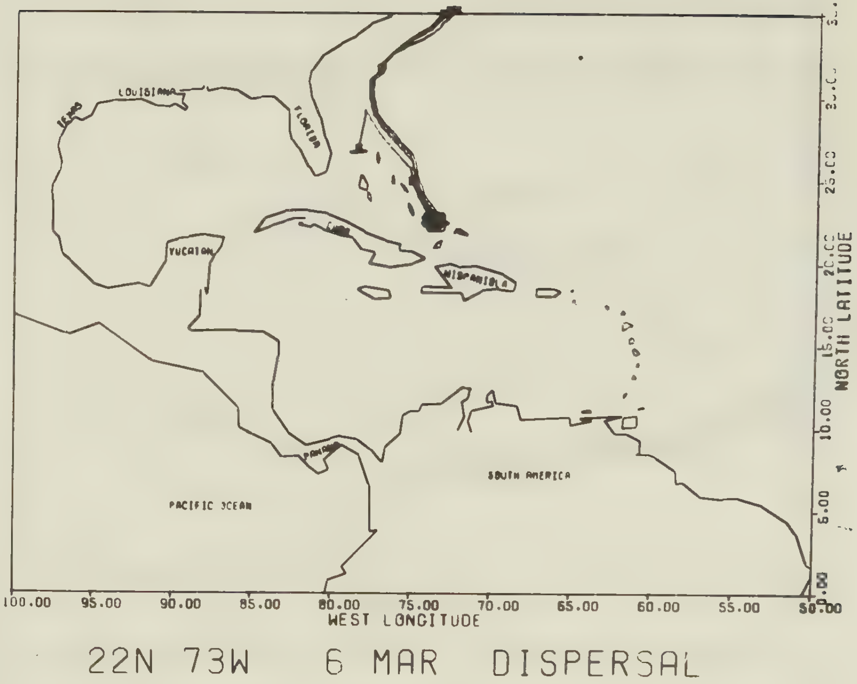
22N 73W 1 MAR DISPERSAL

Fig. 5 Computer generated drift paths for the following one degree square, date and type of path: 22°-23°N: 73°-74°W, 1 March, dispersal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22N 73W 6 MAR DISPERSAL

Fig. 6 Computer generated drift paths for the following one degree square, date and type of path: 22°-23°N:73°-74°W, 6 March, dispersal

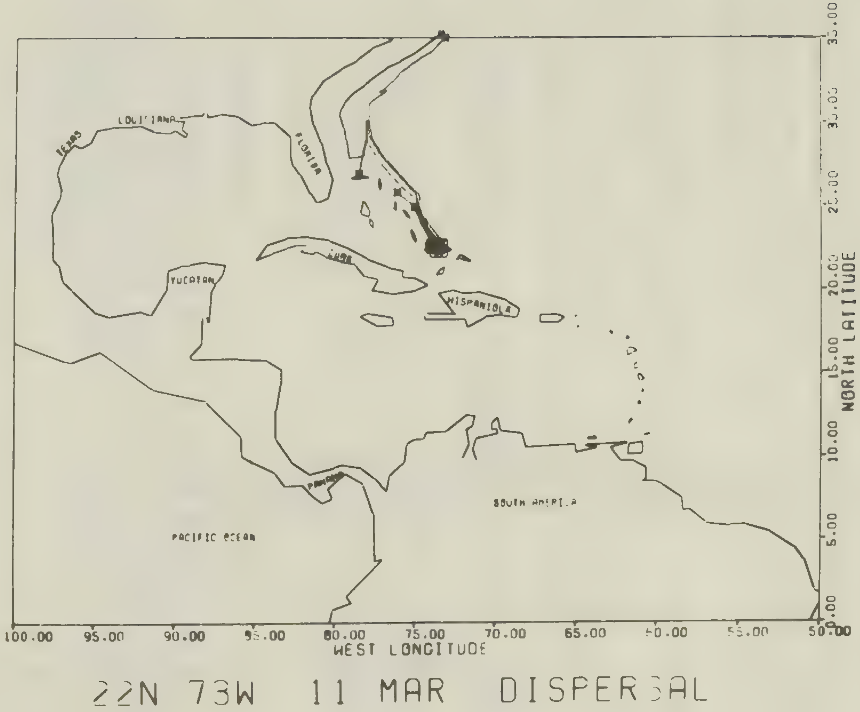
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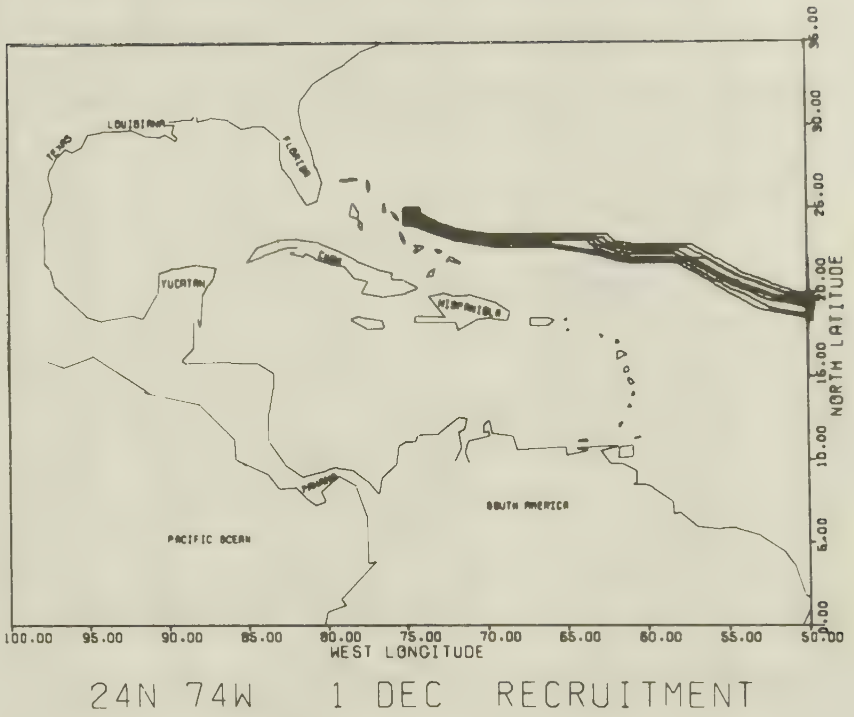
Fig. 7 Computer generated drift paths for the following one degree square, date and type of path: 22°-23°N: 73°-74°W, 11 March, dispersal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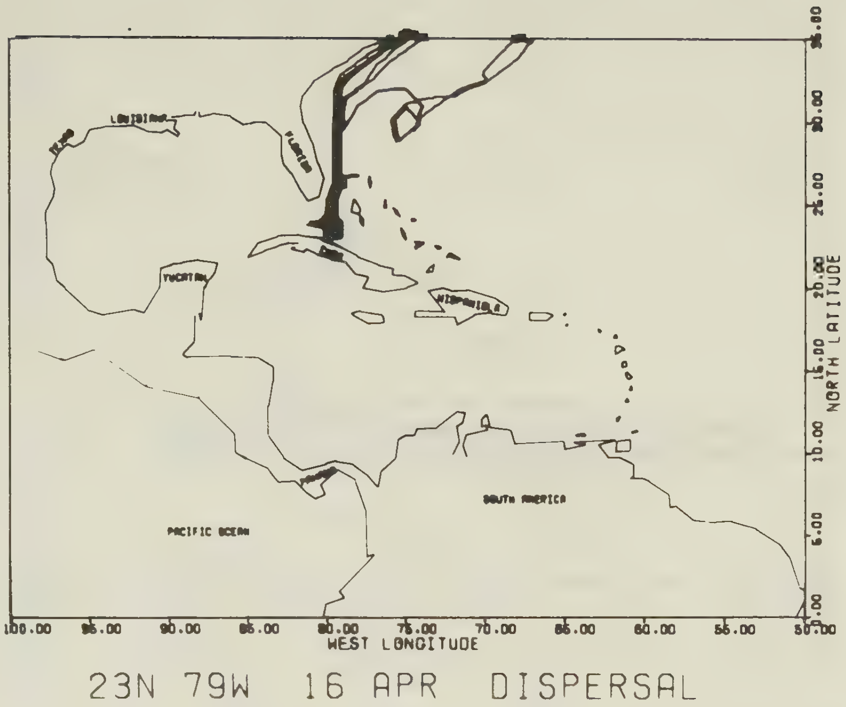
24N 74W 1 DEC RECRUITMENT

Fig. 8 Computer generated drift paths for the following one degree square, date and type of path: 24°-25°N:74°-75°W, 1 December, recruitment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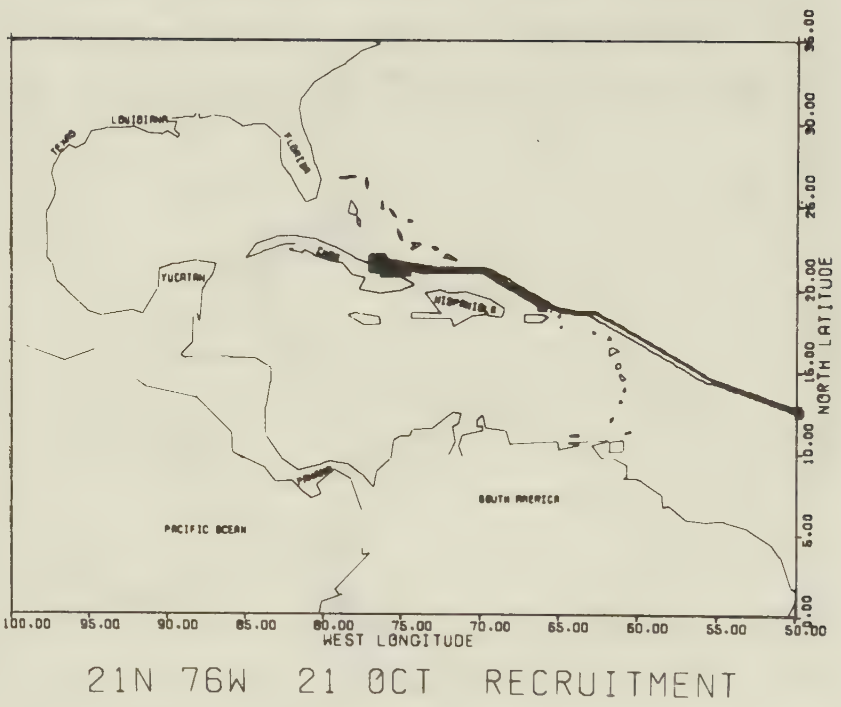
23N 79W 16 APR DISPERSAL

Fig. 9 Computer generated drift paths for the following one degree square, date and type of path: 23°-24°N: 79°-80°W, 16 April, dispersal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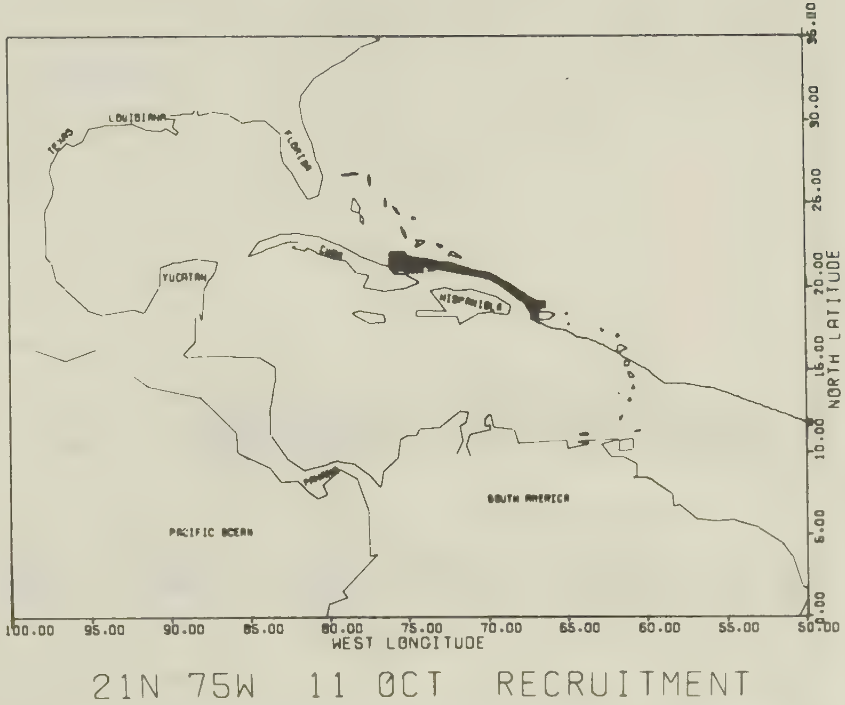
21N 76W 21 OCT RECRUITMENT

Fig. 10 Computer generated drift paths for the following one degree square, date and type of path: 21°-22°N:76°-77°W, 21 October, recruitment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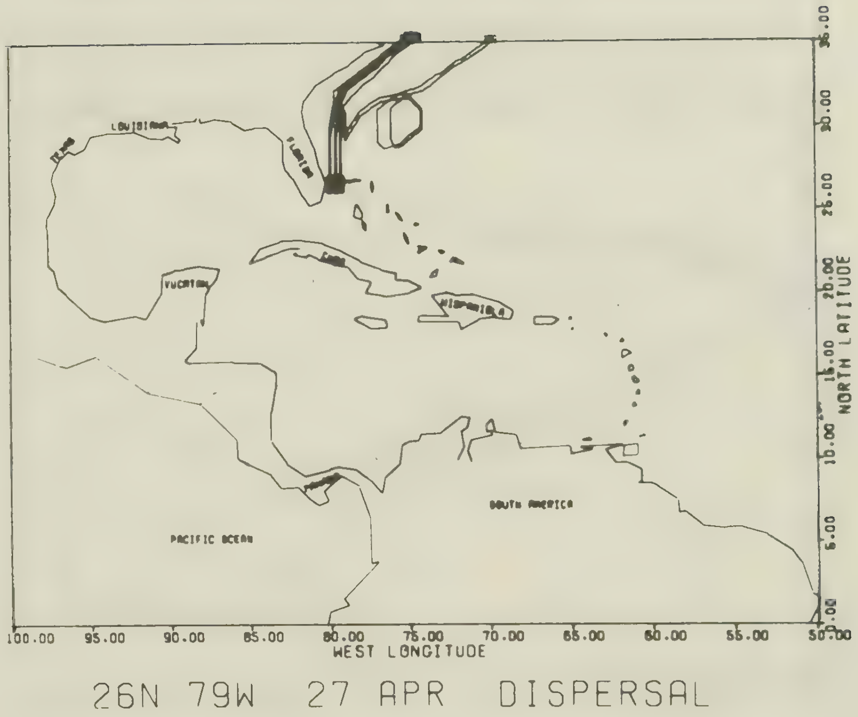
21N 75W 11 OCT RECRUITMENT

Fig. 11 Computer generated drift paths for the following one degree square, date and type of path: 21°-22°N: 75°-76°W, 11 October, recruitment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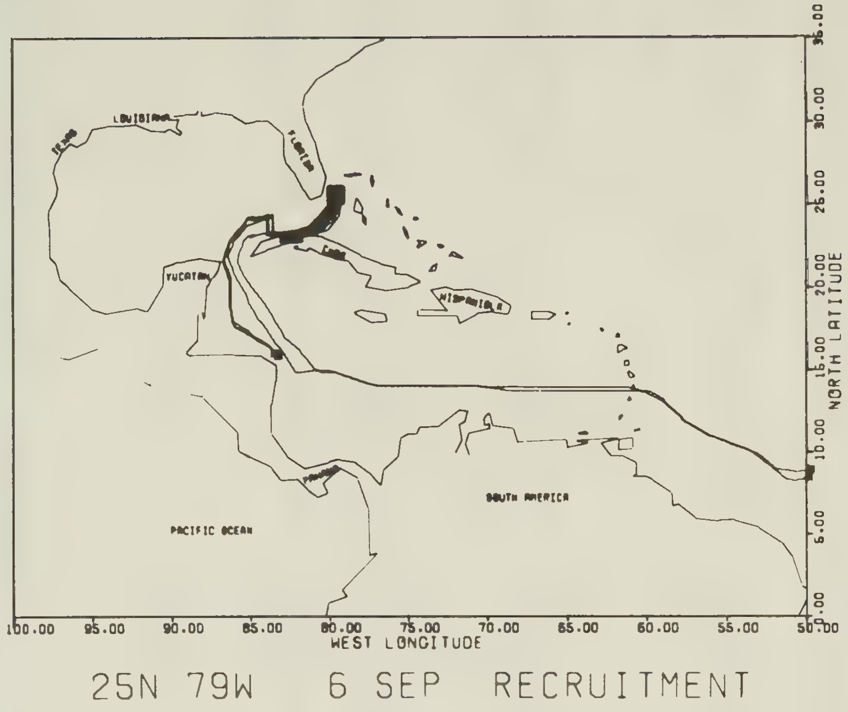
NORTH LATITUDE
26N 79W 27 APR DISPERSAL

Fig. 12 Computer generated drift paths for the following one degree square, date and type of path: 26°-27°N:79°-80°W, 27 April, dispersal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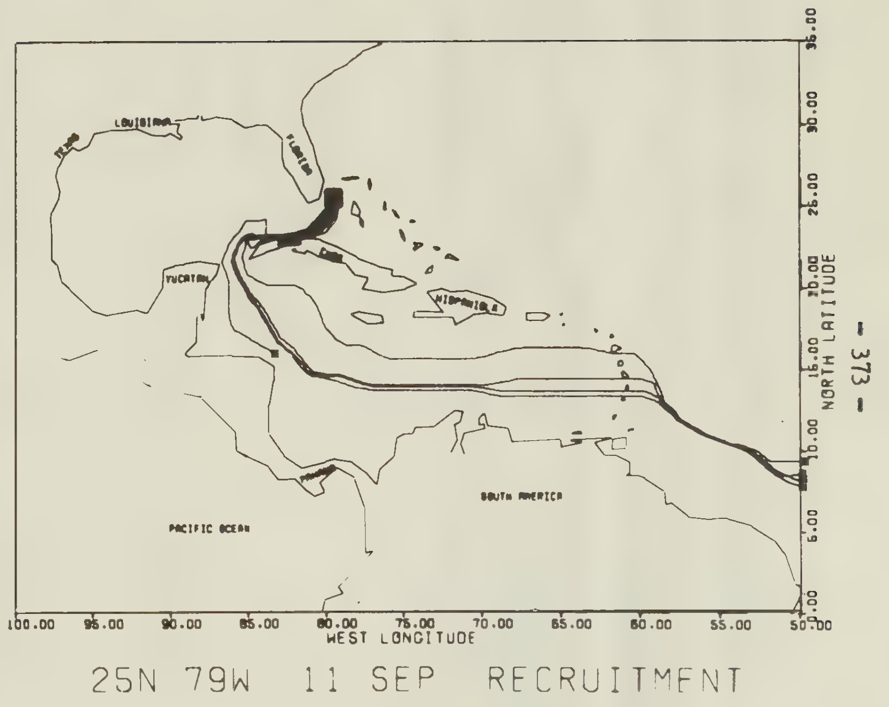
25N 79W 6 SEP RECRUITMENT

Fig. 13 Computer generated drift paths for the following one degree square, date and type of path: 25°–26°N: 79°–80°W, 6 September, recruitment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25N 79W 11 SEP RECRUITMENT

Fig. 14 Computer generated drift paths for the following one degree square, date and type of path: 25°–26°N:79°–80°W, 11 September, recruitment

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BRIEF REVIEW OF ACTIVITIES CONCERNED WITH MARINE RESOURCES RESEARCH CONDUCTED BY UNDP/FAO PROJECTS IN THE WESTERN CENTRAL ATLANTIC

by

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2. MAJOR PROJECTS COMPLETED
3. OPERATIONAL PROJECTS
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Abstract

The United Nations Development Programme (UNDP) and the Food and Agriculture Organizatio of the United Nations (FAO) have, for the last twenty-five years, given assistance to most of the countries of the Western Central Atlantic in developing and managing their fisheries.

This paper briefly reviews the activities of major projects which have been completed during the last five years and of those still in operation in resources research.

Annex I contains information on the objectives of the projects considered.

Resumen

El Programa Especial de Naciones Unidas para el Desarrollo (PNUD) y la Organización de las Naciones Unidas para la Agricultura y la Alimentación (FAO) en los ultimos 25 años han estado otorgando asistencia para el desarrollo y administración de las pesquerías a la mayoría de los países del Atlántico centro occidental.

Este documento revisa en forma resumida las actividades desarrolladas en los proyectos más importantes sobre investigación de recursos que han sido terminados en los últimos 5 años y de aquellos que actualmente se encuentran en ejecución.

El anexo I contiene información sobre los objectivos generales de los proyectos señalados anteriormente.

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1. INTRODUCTION

The United Nations Development Programme (UNDP) and FAO, recognizing the need to improve knowledge of marine fishery resources of the Western Central Atlantic in order to accelerate development of its fisheries, for the last twenty-five years have been giving assistance to most countries of the area with a series of projects. On both a regional and a national basis, assistance has been given on resources research, resources surveys and evaluation, exploratory and experimental fishing, aquaculture, and training in these fields. This paper gives some brief information on these activities. Assistance was given also in other sectors of fisheries not reviewed here. Further information on objectives of the projects is given in Annex I. The UNDP input to the projects considered was about U.S.$ 20 million. The Government contributed around U.S.$ 22 million. Many projects have been completed, others are operational, and yet others are being considered. They are dealt with in this paper accordingly. Although many have been completed, only major projects completed during the last five years are considered. Results of project investigations completed or in operation have been considered by Klima (1976) and Wise (1976); their studies are available to the Symposium.

2. MAJOR PROJECTS COMPLETED

2.1 Caribbean Fisheries Development Project

The Caribbean Fisheries Development Project conducted extensive exploratory and experimental fishing operations in the Caribbean Sea from the edge of the Central American continental shelf east to the arc of the Lesser Antilles. In the Atlantic Ocean adjacent to the Caribbean, some explorations were made in the waters near Hispaniola, Puerto Rico and the Lesser Antilles. The continental shelf off north-eastern South America between Margarita Island, Venezuela, and the border between French Guiana and Brazil was also explored. Territorial and adjacent waters of the Central American countries, Colombia and Venezuela were not investigated as they fell within the study area of other UNDP/FAO projects considered under (b), (d) and (g).

Operations were carried out for about five years (November 1966 to August 1971) by three multi-purpose vessels adaptable to longlining, trawling, live bait/pole-and-line fishing, trap fishing, reel fishing, trolling and gillnetting. Accommodation was provided for fishermen trainees.

The total effort of nearly 2 500 days resulted in a total catch of about 540 000 kg; nearly 450 000 kg were foodfish. Of the foodfish total, nearly three quarters was of demersal species taken by trawl, handline or reel, and pots. Effort for these species was almost one half of the total. Over one fifth of the total effort was devoted to live bait/pole-and-line fishing, but this yielded only about 3 percent of the total catch. Further details on the results of the operations are found in NOAA/NMFS (1974).

2.2 Central American Fishery Development Project

This project served the five countries of Central America and Panama.

Exploratory and simulated commercial fishing operations were conducted on the Atlantic continental shelf within, and beyond, the traditional fishing grounds of Guatemala, Honduras, Nicaragua, Costa Rica and Panama to investigate distribution and abundance of shrimp and lobster resources. These investigations were carried out during different periods from 1968 to 1971 by a multi-purpose vessel adapted to trawl, shrimp and trap fishing for shrimp and lobsters. Observations were made also on abundance of Norway lobsters and fish. Details of these operations are given by Giudicelli (1971 and 1971a), and Yesaki and Giudicelli (1971).

2.3 Marine Biology Project - Belize

Various aspects of the spiny lobster (*Panulirus argus*) fishery in Belize waters were studied by four FAO experts over a period of about five years as indicated by Baird (FAO/UN, 1973b). Subsequently, in accordance with a request from the Government, further assistance was provided under a UNDP/FAO project from September 1969 to April 1972 on management of fisheries resources with particular reference to the spiny lobster.

During that project, returns of tagged lobsters were analysed, tagging experiments initiated with conch (Strombus gigas) to determine growth rates and movements, the method of statistical collection was reviewed and modified, and the economic feasibility of deep-water fishing with electric reels was studied based on results from cruises made by a vessel of the project.

2.4 Marine Fisheries Development Project - Colombia

This was implemented by the Colombian Government and FAO from January 1968 to December 1973. The purpose was to assist in the development of marine fisheries through advisory services, surveys, experimental fishing and training of fishery biologists and fishermen. It encompassed both coasts of Colombia.

Exploratory fishing operations were carried out along the Caribbean coast during various periods during 1969 and 1970 using a project vessel equipped with purse seines, trawls, shrimp nets, longlines and acoustic equipment. The purpose was to determine the fishing potential of fish, shrimp and spiny lobsters in the various areas surveyed. Details of results are given by Squires et al. (1974 and 1974a), Testaverde et al. (1972), and Ben-Tuvia and Rios (1974).

2.5 Fisheries Development - Cuba

Some objectives of this project, in operation from August 1972 to December 1974, were: to plan and execute research on stocks of fish and shellfish of interest to the Cuban fisheries and to evaluate these resources as a basis for development and management; to train scientific and technical personnel; to plan and execute research on marine pollution in relation to fishery resources; to improve aquaculture in mangrove and lagoon areas with special reference to oyster and shrimp resources.

The project assisted in studies of fish resources on the Campeche Bank, shrimp resources, oysters, shrimp culture and in a programme of pollution investigation. A comprehensive list of documents prepared during the project is given in FAO/UN (1975).

2.6 Fishery Research and Development Project - Mexico

The objectives of this project, which was in operation from November 1969 to October 1974, were to assist the Government of Mexico in the development of Mexican fisheries through resources surveys, biological investigations, experimental fishing and improvement of fishing gears and fishing techniques, studies on economics and statistics, data processing, training, and other related activities.

Although project activities were carried out mainly along the Pacific coast of Mexico, relatively extensive work in the fields of physical and biological oceanography was conducted on both Atlantic and Pacific coasts, using three research vessels. Physical oceanography studies were oriented principally toward establishing the structure of water masses, and their dynamics in the Gulf of California and the Gulf of Mexico. Biological studies were directed principally toward studying the distribution of fish eggs and larvae, using this as a means of obtaining global estimates of the size of important fish stocks. During the oceanographic studies, the project participated in research surveys coordinated by CICAR.

The project assisted with various programmes related to aquaculture and participated with the Secretaría de Recursos Hidráulicos of Mexico in a cooperative planning study on research required to develop the use of the coastal lagoons.

Extensive training was provided on fisheries biology, acoustic fisheries biology, acoustic fish-finding, stock assessment, statistical methods and computer programming. A small number of long-term, and a larger number of short-term fellowships were given. Further information on project activities and results are given in FAO/UN (1975a).

2.7 Fisheries Research and Development Project - Venezuela

This was implemented by the Venezuelan Government and FAO from December 1967 to December 1972. It was able to undertake a wide range of studies of marine fishery resources and evaluate the major resources then under exploitation. A detailed evaluation of exploitation levels until the end of 1971 was made by Griffiths and Simpson (1972).

In spite of the lack of fisheries research vessels, some experimental fishing for sardines and other fish was carried out using a small drum seiner.

Six exploratory trips were made with a chartered trawler in the inner Gulf of Venezuela and the Lake of Maracaibo.

Nineteen hydro-acoustic surveys were undertaken, using a converted Florida shrimp trawler.

Several studies of the marine environment were made to determine, as far as possible, the main features that could be related to fish distribution and abundance. These studies were, mainly, in conjunction with fish egg and larvae surveys, and acoustic surveys.

A report on coastal upwelling and other oceanographic features was prepared by Griffiths and Simpson (1972a). These authors also studied upwelling and biological production in the Gulf of Cariaco, one of the main sardine fishery areas in eastern Venezuela (Simpson and Griffiths, 1971).

Data production during the project greatly exceeded the capacity available to analyse or even appraise them; a system for automatic data processing was, therefore, developed.

The results of project activities were published serially in the following bulletins: Fishery Resources and Exploitation Series, Technical Reports and Fisheries Publications. Several papers were also published as part of the documentation of the first CICAR Symposium, and in the Proceedings of the Gulf and Caribbean Fisheries Institute.

3. OPERATIONAL PROJECTS

3.1 International Project for the Development of Fisheries in the Western Central Atlantic (WECAF)

The purpose of this project is to coordinate efforts for fisheries development in the Western Central Atlantic; it will facilitate the participation of all countries having an interest in fisheries in the region, including those from outside the region.

The two main objectives are: firstly, to assist in ensuring the full and rational exploitation and utilization of the resources in the Western Central Atlantic through the development of fisheries of underexploited stocks; secondly, the promotion of appropriate management action for stocks which are heavily exploited. For both these objectives, the project will act as a coordinating mechanism, will advise on the harmonization of fishery policies and action at national and regional level, and will facilitate the provision of international assistance.

The preparatory phase of the project was started on 1 March 1975; it was endorsed by 26 countries and territories.

During this phase, seven consultants were engaged to assist in preparing the operational phase. Several studies were prepared, two of which - Klima (1976) and Wise (1976) - are available to the CICAR II Symposium.

The document for the operational phase has been submitted to UNDP for approval. This phase should become operational in January 1977. It is proposed that the project should be of five years duration and its activities encompass statistics, monitoring of resources, resources management and identification of development opportunities, fishery development, coastal aquaculture, fisheries training and education, and fisheries administration and legislation. For the duration of the project, these activities would be carried out by an international staff of seven specialists supported by a large number of consultants.

The project provides for support from external donors, e.g., bilateral agencies, to assist in both improving the effectiveness of inshore artisanal fishing and a survey to assess pelagic resources of the Western Central Atlantic in order to determine their potential development.

Coordination will be by the Western Central Atlantic Fishery Commission (WECAFC) established by FAO in November 1973.

Some project specialists will collaborate closely with Working Parties established by WECAFC at its first session (Port of Spain, October 1975), namely the Working Party on Fishery Statistics, Working Party on Assessment of Fish Resources and Working Party on Stock Assessment of Shrimp and Lobster Resources (WECAFC, 1975).

3.2 Fishery Development Study - Bahamas

The first phase was initiated in June 1972; it will be completed in June 1976. An extension (second phase) for another three years is under consideration.

A main objective was to carry out an intensive exploratory fishing programme aimed at identifying and evaluating stocks of fish and shellfish, particularly spiny lobster. Data analysis from exploratory electric reel fishing off the edge of the Bahamian banks, carried out from 1972 to 1974, was made by González Alberdi (1975).

3.3 Fishery Research and Development - Brazil

The operation of this project was initiated in April 1970 and will be completed by the end of 1976.

Surveys of demersal, semipelagic and pelagic fish stocks and shrimp resources were carried out by six vessels along the coast of Brazil as well as assessment of shrimp, sardine and stocks of sciaenids. Systems for collection of statistics and data processing have been developed. The project has issued various documents containing information on work being carried out.

3.4 Caribbean Fisheries Training and Development Institute - Barbados, Trinidad and Tobago, Guyana

Since 1974 the Institute has been established to train personnel in all sectors of modern fishing including collection of statistics and biological data. Particular emphasis is given to training for industrial fishing for shrimps. The first group of about 45 students completed their training recently. The Institute will collaborate closely with the WECAF project.

3.5 Culture of Brackish Water and Marine Fishes - Cuba

This project was initiated in April 1974 and will be in operation for three years in order to assist the Government of Cuba in developing techniques for brackish water and marine fish culture. Experiments are being conducted on induced breeding and culture of mullet, and introduction and culture of milkfish (*Chanos chanos*).

3.6 Commercial Fisheries Training - Jamaica

This project is of three years duration, June 1974-May 1977. Main objectives are to train personnel for a commercial offshore fleet; to train artisanal fishermen to operate a modern offshore commercial fishery; to exploit new, confirmed fish resources within range of offshore fishing vessels; to increase local fish production.

4. PROJECTS UNDER CONSIDERATION

Requests for assistance have been received from Grenada, Honduras, Panama, St. Lucia and St. Vincent.

5. OBJECTIVES OF THE PROJECTS CONSIDERED IN THE TEXT[1]

5.1 Major Projects Completed

Caribbean Fisheries Development Project

(i) Exploratory fishing
(ii) Marketing and demonstration
(iii) Training
(iv) Fishery development and advisory services

Central American Fishery Development Project

(i) Strengthening of fishery administration and planning
(ii) Development and management of various fisheries
(iii) General resources survey
(iv) Improvement of processing and marketing

Marine Biology Project - Belize

Advice on the management of fishery resources with particular reference to the spiny lobster (Panulirus argus)

Marine Fisheries Development Project - Colombia

(i) Assistance to Government and industry in strengthening the fishery administration, in reviewing factors affecting the development of the industry and in organizing fishery research

(ii) Surveys and experimental fishing to assess the available resources and develop efficient methods of exploiting them

(iii) Assistance to the Government in defining a fishery policy and establishing a fisheries development plan compatible with the overall economic development strategy of the Government

(iv) Assistance in the implementation of selected projects of fisheries development, particularly those concerned with artisanal fisheries

Fisheries Development - Cuba

(i) Assistance to the Government in planning and execution of biological research on the stocks of fish and shellfish of interest to the Cuban fisheries, and the evaluation of those resources as a basis for their development and management, as well as training of scientific and technical personnel in these fields

(ii) Training of fishermen, skippers and gear technologists in modern methods of fish-finding and capture

(iii) Development of fishing methods and gear particularly suited to local conditions

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[1] Although no specific reference is made to training in the objectives of some projects, training of counterparts to international staff and on-the-job training is a major element of all projects. Fellowships for specialized training are also awarded

(iv) Planning and execution of research on marine pollution in relation to the living resources

(v) Improvement of aquaculture in mangrove and lagoon areas with special reference to oyster and shrimp resources

Fishery Research and Development Project - Mexico

(i) Advice to Government and industry to further the fisheries of the country; cooperate with the Government in its programme of research, development and conservation of the shrimp resource

(ii) Assistance in solving problems related to fish processing and utilization

(Other objectives referred specifically to the Pacific coast)

Fisheries Research and Development Project - Venezuela

(i) Survey of coastal demersal and pelagic fish stocks

(ii) Biological evaluation of marine resources to determine the potential of fishery development

(iii) Exploratory and experimental fishing

(iv) Fishery statistics

(v) Processing technology

(vi) Marketing

(vii) Naval architecture

(viii) Fisheries administration

(ix) Fisheries legislation

5.2 Operational Projects

International Project for the Development of Fisheries in the Western Central Atlantic (WECAF)

(i) Resource monitoring

    (a) Statistical and biological data

    (b) Research

(ii) Resource utilization

    (a) Resource management and identification of development opportunities

    (b) Resource exploitation

(iii) Fishery administration and legislation

    (a) To assist in strengthening fishery administration in general and national fishery research and development in particular

    (b) To assist in formulating fishery legislation

(iv) Training

At all levels, in all fishery sectors

Caribbean Fisheries Training and Development Institute - Barbados, Trinidad and Tobago, Guyana

(i) Assistance to Governments in setting up a permanent Fisheries Training and Development Institute to provide skilled personnel in all sectors of a modern fishing industry

(ii) Assistance in implementing national fisheries development plans

(iii) Training counterpart staff for the Institute

Fishery Development Study - Bahamas

(i) Exploratory fishing aimed at identifying and evaluating available fish, particularly spiny lobster, and other marine resources

(ii) Demonstration of improved fishing techniques which could be adopted by the local industry

(iii) Advice and demonstration of handling, distribution and marketing of fresh and frozen fish and crustacea

(iv) Advice on necessary Government organization and administration, and institutional framework (credit, cooperatives, etc.) to assist in accelerated fisheries development

Fishery Research and Development - Brazil

(i) Assistance in analysis of projects to receive financial support under development incentive legislation, and in the implementation of the National Fisheries Plan

(ii) Assist the industry in planning and executing development schemes

(iii) Appraisal of pelagic and demersal stocks with initial emphasis on sardine, menhaden, mullet, jack mackerel, bonito, bluefish and certain demersal species, croaker in particular

Culture of Brackish Water and Marine Fishes - Cuba

(i) Survey of coastal lagoons to determine suitability for aquaculture

(ii) Selection of suitable local species of fish and shellfish for aquaculture

(iii) Pilot-scale studies in aquaculture to determine the technical and economic feasibility of aquaculture under local conditions

(iv) Assistance in formulation of aquaculture development programmes

(v) Training local personnel in methods of aquaculture in lagoons

Commercial Fisheries Training - Jamaica

(i) Training captains, engineers and fishermen for a commercial offshore fishing fleet

(ii) Promotion of fish production by exploitation of new, confirmed fish resources within range of offshore fishing vessels

(iii) Increase local production, to reduce the volume of foreign imported fish

(iv) Training fishermen from mechanized canoe fisheries to increase their earnings by participation in a modern offshore commercial fishery

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ESTUDIO SOBRE LA FIJACION DE LARVAS DE MEJILLON, PERNA PERNA, EN LAS ENSENADAS DE LA ESMERALDA Y GUATAPANARE (ESTADO SUCRE, VENEZUELA)

por

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CONTENIDO

1. INTRODUCCION
2. MATERIALES Y METODOS
3. RESULTADOS
4. DISCUSION Y CONCLUSIONES
5. REFERENCIAS

Resumen

Se estudió la variación mensual de la fijación de la larva del mejillón, *Perna perna*, en las ensenadas de La Esmeralda y Guatapanare (Estado Sucre), durante el período comprendido entre septiembre de 1971 y noviembre de 1975.

El período de mayor fijación se observó entre los meses de enero-abril. Igualmente se observó que el período de mayor fijación coincidió con el período de temperatura más baja en el agua superficial.

Abstract

Studies were carried out on the monthly variation in settlement of *Perna perna* in the areas of the most important natural beds, the La Esmeralda and Guatapanare inlets, from September 1971 to November 1974.

The January-April period was observed to be the most important, showing the biggest recruitment and coinciding with the lowest surface temperature.

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1. INTRODUCCION

En la actualidad el mejillón, Perna perna, se cultiva en Venezuela por los sistemas de balsas flotantes y parques fijos (Salaya et al., 1973).

La producción de mejillón cultivado durante los últimos cinco años fue la siguiente:

Años:	1971	1972	1973	1974	1975
Toneladas:	93	187	260	250	258

Los trabajos realizados sobre la reproducción y fijación del mejillón nos dan la siguiente información: Romero (1966) encontró la mayor fijación en el mes de enero; Vélez y Martínez (1967) concluyen que la reproducción de esta especie se efectúa todo el año, pero con mayor intensidad durante el período de enero a abril; Carvajal (1969) encuentra tres períodos de desove intensos en los meses de septiembre-diciembre, febrero y abril-junio. Benitez y Okuda (1971) encontraron que entre noviembre y marzo es la época más intensa de desove; Vélez (1971), al analizar la fluctuación del índice de engorde asociada con el ciclo reproductivo, encuentra tres períodos de desove: octubre-enero, febrero-abril y julio-agosto.

Además Vélez (op. cit.) dice que por experiencia de campo se ha demostrado que la mayor abundancia de juveniles se presenta de febrero a marzo.

Uno de los problemas planteados que puede limitar la expansión del cultivo del mejillón es la escasez de semilla (Salaya, 1974). Toda semilla utilizada en el cultivo hasta 1974 fue extraída de las rocas y acantilada en la zona intermareal de los bancos naturales comprendidos entre La Esmeralda y Carúpano, Estado Sucre.

De acuerdo con Romero (1966) y Salaya et al. (1973) se han realizado ensayos exitosos para la recolección de semilla (juveniles) de mejillón usando colectores artificiales de cuerdas de sisal, esparto, caucho y varas de guatacare (Beureria cumanensis), colocados horizontal y verticalmente en balsas ubicadas en los bancos naturales de la costa norte del Estado Sucre.

Los resultados anteriores condujeron a que el Ministerio de Agricultura y Cría, dictase la resolución No. 337 del 3 de julio de 1974 (Anexo 1), la cual obliga a toda persona o empresa que se dedique al cultivo del mejillón, a instalar colectores artificiales de semilla. A los efectos, dos de las empresas cultivadoras instalaron dos parques fijos de 1 000 m^2, aproximadamente para la recolección de semilla de La Esmeralda. Es interesante señalar que el Gobierno Nacional a través del Instituto de Crédito Agropecuario, aprobó un crédito para la instalación de 250 balsas de cultivo para una producción estimada de 5 340 t por año. Para la siembra de esas 250 balsas se ha estimado que se necesitarán 837,5 t de semilla, lo cual es más del doble de la producción total nacional de mejillón para 1974 que fue de 383,5 t.

En el presente trabajo se estudió la fluctuación de la fijación de la larva del mejillón desde agosto de 1971 hasta noviembre de 1974. Consideramos que los resultados obtenidos serán de valiosa ayuda para los cultivadores, quienes deben de conocer el momento más apropiado para poner los colectores artificiales y lograr la mayor captación de semillas para sus cultivos.

2. MATERIALES Y METODOS

Las ensenadas de Guatapanare y La Esmeralda están localizadas en la costa norte del Estado de Sucre, en la zona de los bancos naturales de mejillón de mayor importancia (Fig. 1).

El control de la fijación fue realizado mediante la reposición quincenal de los colectores desde agosto 1971 hasta noviembre de 1974.

Los colectores se elaboraron con conchas o valvas de mejillón (Perna perna) y concha peregrina (Pecten papyraceus), colocadas entre láminas de tela plástica de 0,25 m^2 con una malla de 2 cm (Fig. 2).

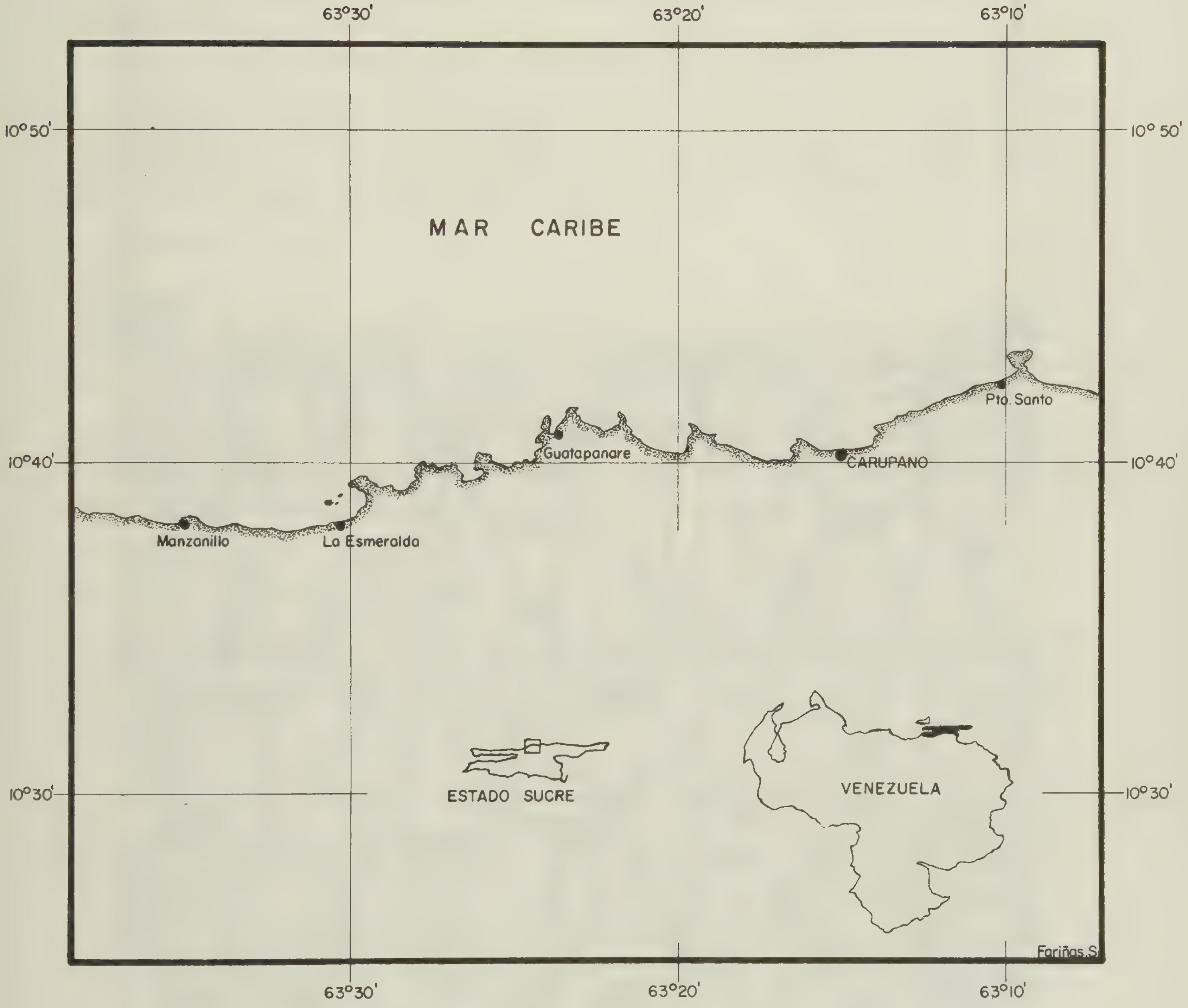
63°30'
63°20'
63°10'
10°50'
10°40'
10°30'
MAR CARIBE
Pto. Santo
Guatapanare
CARUPANO
Manzanillo
La Esmeralda
ESTADO SUCRE
VENEZUELA
Fariñas S.

Fig. 1 Situación geográfica de las ensenadas de La Esmeralda y Guatapanare

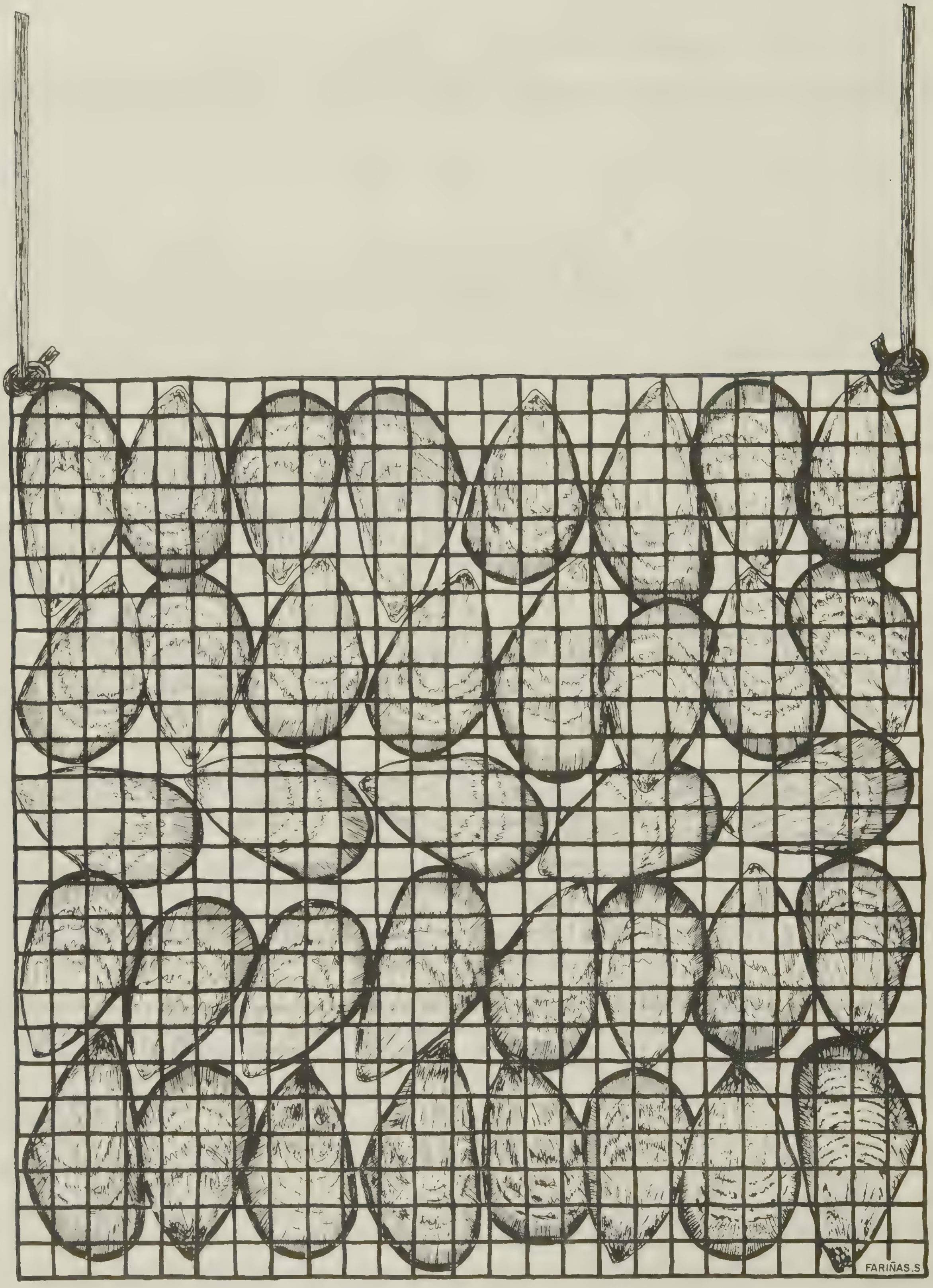

Fig. 2 Colector de conchas de mejillón utilizado para la fijación larval

En cada estación se colocaron dos colectores superficiales (50 cm por debajo de la superficie del mar aproximadamente) que colgaban verticalmente de una balsa experimental. De cada colector se muestrearon al azar diez conchas en las cuales se observó la fijación en ambas caras.

En cada concha se marcaron cuatro subáreas (dos por cada lado) de 1,5 cm^2 cada una.

La observación y contaje de los pequeños reclutas se efectuó con una lupa estereoscópica.

Simultaneamente con los registros de fijación se midió directamente la temperatura del agua superficial con un termómetro de 0,1°C de precisión. Posteriormente se hizo un promedio con las diferentes mediciones hechas durante cada mes.

3. RESULTADOS

3.1 Temperatura

En las Figs. 5 y 6 se observa que los cambios estacionales en la temperatura superficial del agua son similares en las dos ensenadas. Los valores mensuales promedios mínimos se observaron durante los meses de enero a mayo y los máximos de septiembre a noviembre.

Los valores de temperatura mínima y máxima observadas durante los tres años fueron 22,0°C (8.3.74) y 38,2°C (2.10.74) respectivamente. Estos resultados fueron similares a los observados por Herrera y Febres (1975) quienes trabajaron en Carúpano, ciudad muy próxima a nuestra área de trabajo.

3.2 Fijación

3.2.1 Periodicidad de las fijaciones

En general la fluctuación en la fijación fue similar en las dos ensenadas durante los tres años, observándose que el máximo asentamiento ocurre en los meses de enero a abril. La Fig. 3 muestra que las máximas fijaciones en Guatapanare durante el año 1972, se observaron en los meses de febrero, marzo y abril, mientras que en los años 1973 y 1974 se observaron en los meses de febrero y marzo.

La Fig. 4 muestra que el máximo reclutamiento en La Esmeralda en el año 1972 se observó en los meses de febrero y abril. En 1973 las máximas se observaron en febrero y marzo, y en 1974 en enero, febrero y marzo. Al promediar los valores de fijación de los distintos meses obtenidos durante los tres años se observa que el período de máxima fijación ocurrió en los meses de enero a abril para las dos ensenadas (Fig. 5 y 6).

Los resultados muestran concordancia con los obtenidos por Romero (1966) quien en Guiria de la Playa y Playa Grande observó que la máxima fijación ocurrió en los meses de enero y febrero. Por su parte, Carvajal (1969) observó la mayor fijación en enero en La Esmeralda y Guatapanare, y Vélez (1971) cita que por experiencia de campo se ha demostrado que la mayor abundancia de juveniles se presenta de febrero a marzo.

3.2.2 Intensidad de la fijación

Al hacer el control de la intensidad de fijación de larvas se observó que la misma que fue mayor en la superficie cóncava de la concha, pero para la obtención de los resultados finales se promediaron los valores encontrados tanto en la superficie cóncava como en la convexa.

En la Fig. 5 y en la Tabla I se puede apreciar que la intensidad de la fijación (por metro cuadrado) fue muy variable en los tres años. En la ensenada de Guatapanare los valores máximos de fijación anual se encontraron en el año 1972, mientras que en la ensenada de La Esmeralda los valores de máxima fijación se observaron en el año 1974.

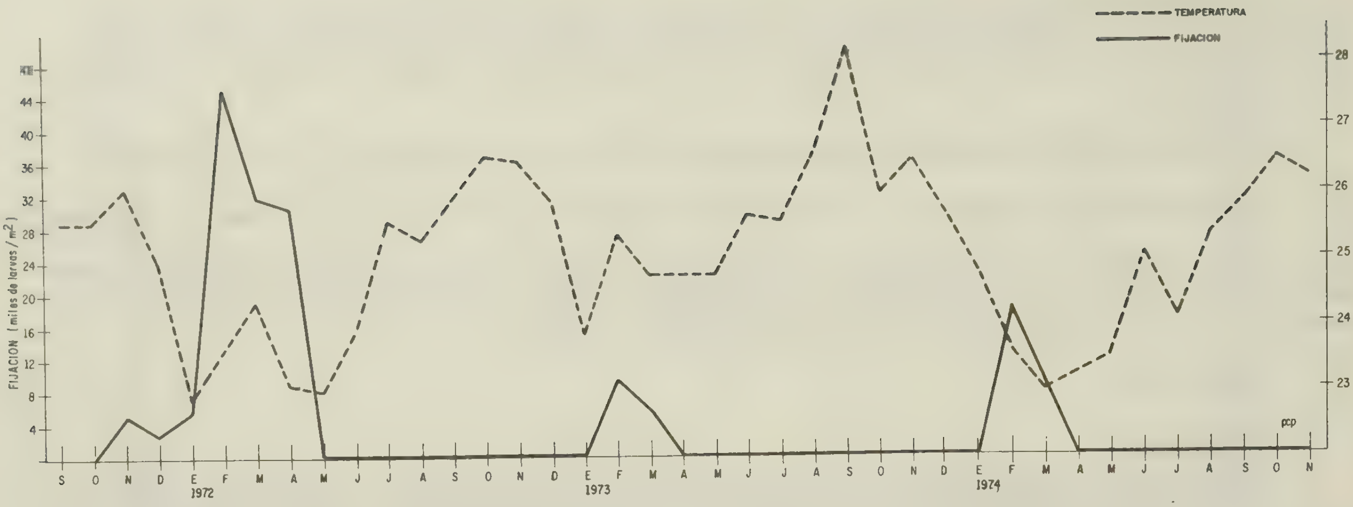

Fig. 3 Fluctuaciones mensuales de la fijación larval y la temperatura superficial en la ensenada de Guatapanare

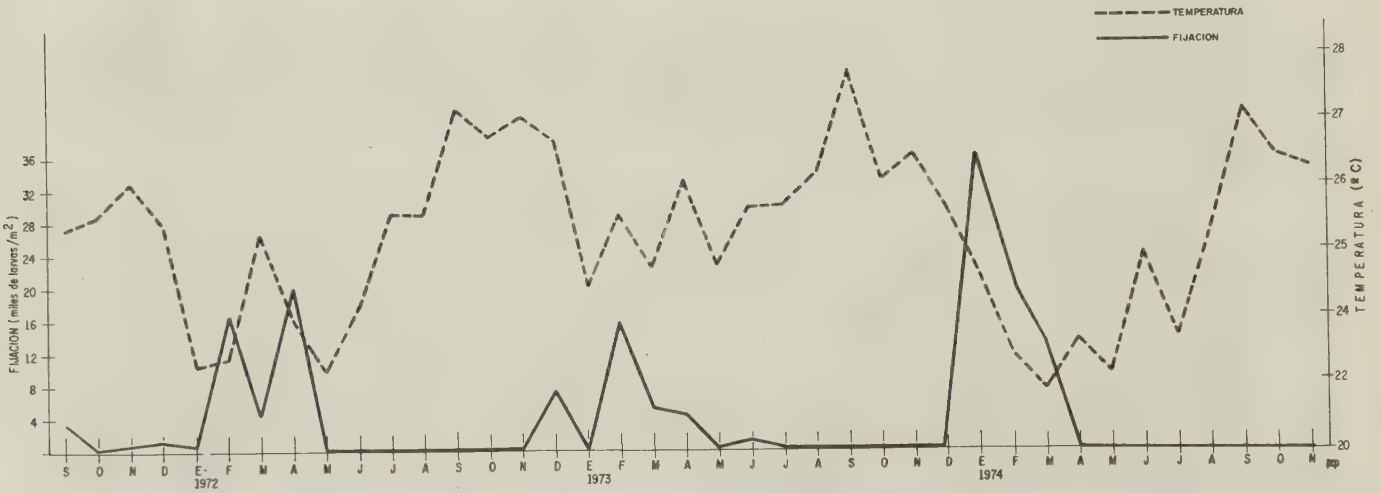

Fig. 4 Fluctuaciones mensuales de la fijación larval y la temperatura superficial en la ensenada de La Esmeralda

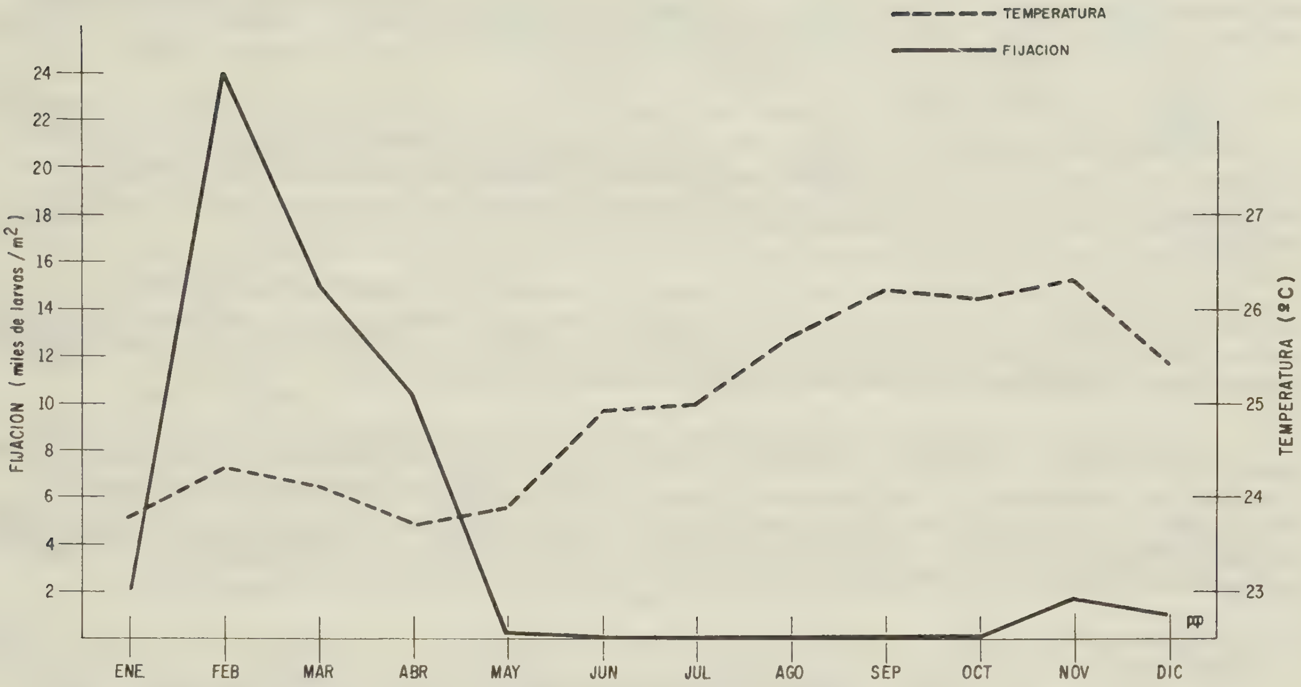

Fig. 5 Fluctuación mensual de los valores promedios de los tres años de la fijación larval y temperatura superficial en la ensenada de Guatapanare

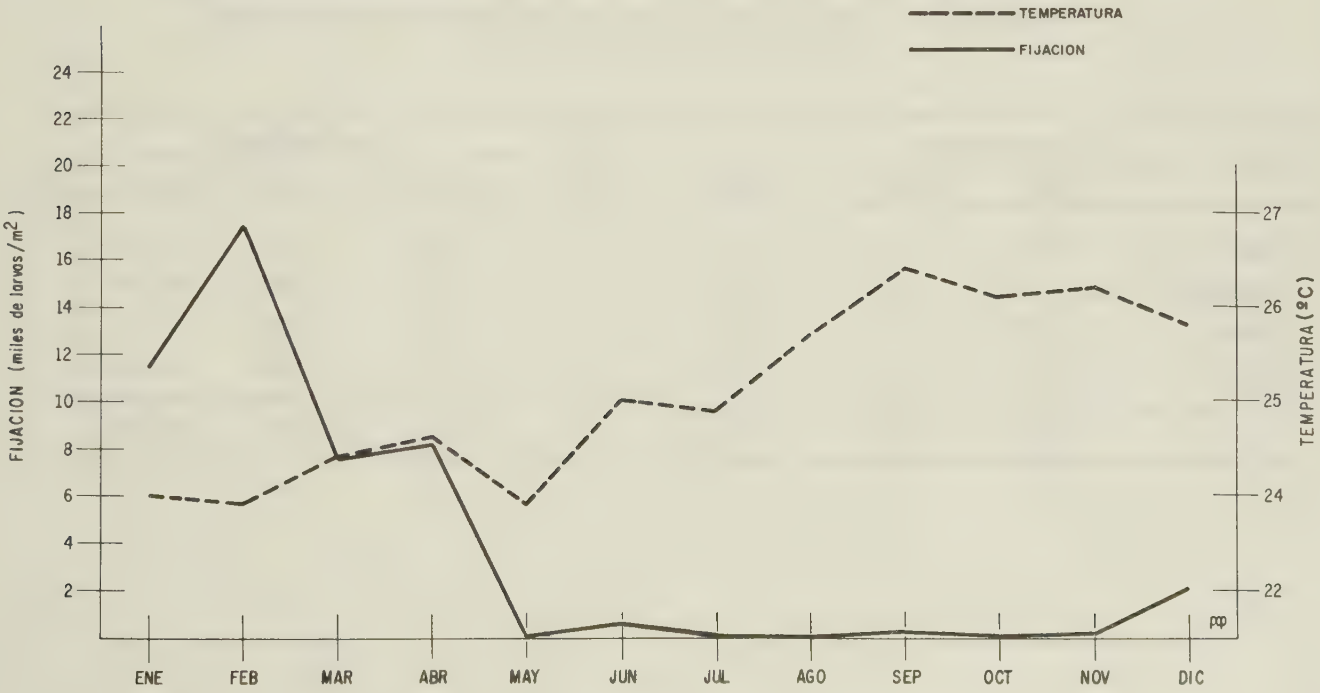

Fig. 6 Fluctuación mensual de los valores promedios de los tres años de la fijación larval y temperatura superficial en la ensenada de La Esmeralda

Al comparar los valores de fijación para el período de enero-abril de las dos ensenadas se observa que en 1972 la fijación en Guatapanare fue mayor que en La Esmeralda, mientras que en los años 1973-74 la fijación fue mayor en La Esmeralda.

4. DISCUSION Y CONCLUSIONES

Los resultados obtenidos durante el período comprendido entre septiembre de 1971 y noviembre de 1974, nos indican que hay un período de máxima fijación que va de enero a abril, por lo que se recomienda a los cultivadores colocar los colectores artificiales en esa época.

En general se ha observado que la fijación de moluscos bivalvos es un proceso que es afectado por muchos factores, así tenemos que diferentes autores que han estudiado este proceso en ostras y mejillones lo han relacionado con temperatura, salinidad, sales de cobre, corrientes, luminosidad, nutrientes, con los períodos de luna, etc.

Los resultados encontrados nos muestran que el período de máxima fijación es coincidente con el período de temperaturas más bajas. Igualmente al correlacionar los datos de fijación con los datos de temperatura, vientos y surgencias dadas por Herrera y Febres, 1975, resulta que el período de máxima intensidad de fijación es coincidente con los períodos de temperaturas más bajas, vientos más intensos y máxima surgencia costera del nororiente de Venezuela (Griffiths y Simpson, 1972).

5. AGRADECIMIENTOS

A los Lic. Anibal Vélez y Amado Acuña, por la lectura crítica del manuscrito y sus valiosas sugerencias. Al Centro de Investigaciones Pesqueras de Oriente del Ministerio de Agricultura y Cría por el financiamiento del trabajo.

TABLA I

Valores estimados de fijación de larvas de mejillón *Perna perna*; individuos por metro cuadrado, en las ensenadas de La Esmeralda y Guatapanare, para el período de máxima fijación (enero-abril) durante los años 1972-73-74

	GUATAPANARE			LA ESMERALDA		
	1972	1973	1974	1972	1973	1974
Enero	5 679	320	641	641	641	33 974
Febrero	45 513	8 333	17 948	16 666	15 385	20 512
Marzo	31 410	5 765	8 333	4 487	5 128	12 820
Abril	30 769	641	320	19 872	4 687	1 602
	113 371	15 059	27 242	41 666	25 841	68 908

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ON A SYSTEMATIC AND ECOLOGICAL STUDY OF THE BOLIVINA VARIABILIS (WILLIAMSON) GROUP (RECENT FORAMINIFERA FROM VENEZUELA)

by

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CONTENTS

1. INTRODUCTION
2. DISCUSSION
3. SPECIES BIBLIOGRAPHY
4. REFERENCES

Abstract

Our collection of recent foraminifera from the inner shelf of Venezuela shows the close affinities that exist between Bolivina variabilis and other species which share a shallow water habitat and exhibit similarities in the characteristics of the wall texture, pores and alveola, as well as in the corrugated ornamentation of the upper margin of the last chamber.

The electron micrographs bring out these similarities - not clearly observable under a binocular microscope - and show that these species belong to the same group, for which we propose the conventional name of Bolivina variabilis.

This group, in spite of its cosmopolitan distribution in the shallow waters of the continental shelves, has been neglected up to now.

Resumen

Nuestras colecciones de foraminíferos recientes de la plataforma interior de Venezuela muestran las estrechas afinidades existentes entre Bolivina variabilis y otras especies que comparten un habitáculo de aguas someras y ofrecen similaridades en las características de la textura de la pared, los poros y las alvéolas, así como en la ornamentación currugada del margen superior de la última cámara.

Las electromicrografías evidencian esas semejanzas - que no se observan claramente bajo el microscopio binocular - y muestran que esas especies forman un grupo, por el cual proponemos el nombre convencional de Bolivina variabilis (Williamson).

Dicho grupo, a pesar de su distribución cosmopólita en las aguas someras de las plataformas continentales, no había sido reconocido hasta ahora.

1. INTRODUCTION

The present paper is based on observations presented originally by the author in a recent monograph of the neontological Bolivinitidae of Venezuela (Sellier de Civrieux, 1976) which included detailed descriptions of 34 species and 8 subspecies of this family of benthonic foraminifera.

The wide scope of that monograph prevented us elaborating on the following group of species, related to Bolivina variabilis (Williamson):

Bolivina variabilis (Williamson)

B. cf difformis (Williamson)

B. pseudoplicata Heron-Allen and Earland

B. rhomboidalis (Millett)

B. tortuosa (Brady)

B. torqueata Cushman and McCulloch

B. ortegai Sellier de Civrieux

B. cf compacta Sidebottom

B. nairi Sellier de Civrieux

B. cf tepida Sliter

B. merecuanai Sellier de Civrieux

For this paper we have collected information and Scanning Electron Microscope electron micrographs of these eleven recent species found in our Venezuelan collection, which point out relationships in the wall texture, in the pore and alveola patterns and in the corrugated ornamentation of the upper margin of the last chamber (apertural side).

2. DISCUSSION

The probable phylogenetic relationship of these species of the Bolivina variabilis group is also supported by our observations on their ecology. These taxa share the same benthic habitat; they frequent the shallower sand and clay bottoms of the inner continental shelves of Venezuela and other regions. Their geographic distribution is wide and, quite probably, cosmopolitan in the neritic zone.

The link between these species of the Bolivina variabilis group has been ignored by previous authors. The reason for this neglect, probably, is that the very small size of the tests, under the binocular microscope, renders difficult the observation of their fine textural and structural features.

Loeblich and Tappan (1957), for instance, proposed to designate Bolivina tortuosa Brady as the type - species of a presumptive new genus, Sigmavirgulina and, consequently, to segregate that species from the genus Bolivina. However, the close relationship of B. tortuosa with the other species of the B. variabilis group is clearly borne out by our electron micrographs, demonstrating that B. tortuosa belongs indeed to Bolivina.

The frequent confusion between different species of the B. variabilis group by authors, and the imprecision of the original diagnosis and iconography of most of the discussed taxa, may also be attributed to the small size of the tests and the consequent limitation of their observation by conventional optics.

Additionally, the range of phenotypic plasticity of each species is wide and leads to interspecific gradations. These have been detailed in our 1976 monograph, together with descriptions of each taxum, the interspecific similarities and differences, as well as the distribution and ecology.

In addition to those recent species, we include tentatively in the Bolivina variabilis group the following:

Recent: Bolivina inflata Heron-Allen and Earland

B. seminula Cushman var. foraminata R.E. and K.C. Stewart

B. advena Cushman

B. quadrata Cushman and McCulloch

B. glutinata Egger

B. cistina Cushman

B. sinuata Galloway and Wissler

Pliocene: Bolivina plicatella Cushman

Miocene: Bolivina hughesi Cushman

Eocene: Bolivina crenulata Cushman

Tertiary: Bolivina hebes Macfayden var. victoriensis Cushman

Some of the specific names of this second list appear to be synonyms of some species of our Venezuela material. It should be pointed out, however, that this is a qualified statement, since we still have reservations in view of the difficulty in interpreting accurately the original descriptions and iconography of some species. For instance, B. plicatella and B. glutinata are probably synonyms of B. pseudoplicata; B. hebes victoriensis; B. sinuata and B. crenulata may represent other synonyms or ancestral forms of B. pseudoplicata. B. subexcavata Cushman and Wickenden is evidently a synonym of B. pseudoplicata. B. inflata and B. quadrata seem to be related to B. compacta, B. variabilis and B. pseudoplicata. B. cistina is closely related to B. torqueata, B. rhomboidalis, B. tortuosa and B. ortegai.

3. SPECIES BIBLIOGRAPHY

The following list of bibliographic references contains the more important information available on the recent species of the Bolivina variabilis group which belong to our Venezuelan collection.

3.1 Bolivina variabilis (Williamson)

(See Figs. 1-3)

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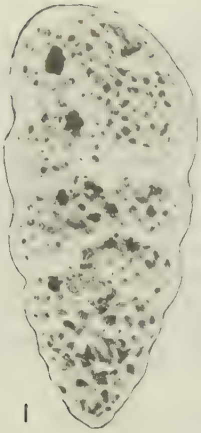
Bolivina variabilis (Williamson) Chaster, 1892, p. 59. Cushman, 1922-a, p. 49, pl. 4, fig. 3-a, b; 1937, p. 158, pl. 16, fig. 6, 12-14; 1949, p. 32, pl. 6, fig. 13-16. Todd and Bronnimann, 1957, p. 33, pl. 8, fig. 31. Voorthuysen, 1960, p. 249, pl. 11, fig. 8. Bermudex and Seiglie, 1963, p. 28, lám. 19, fig. 5. Sliter, 1970, p. 166, pl. 5, fig. 4; pl. 6, fig. 1-3; pl. 8, fig. 15, 16. Murray, 1971, p. 113, pl. 46, fig. 1-3. Haynes, 1973, p. 141, pl. 10, fig. 8; pl. 11, fig. 8, text-fig. 25 (16). Sellier de Civrieux, 1976, p.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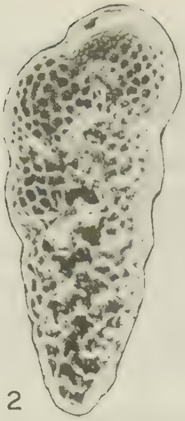
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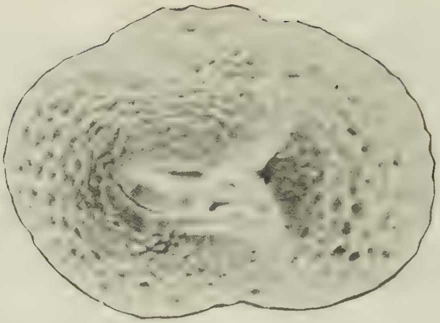
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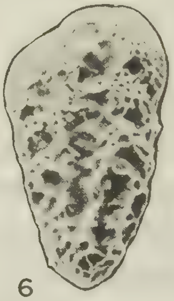
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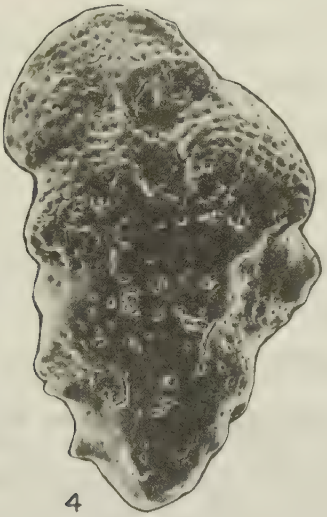
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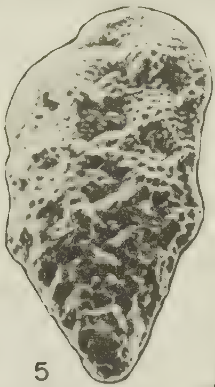
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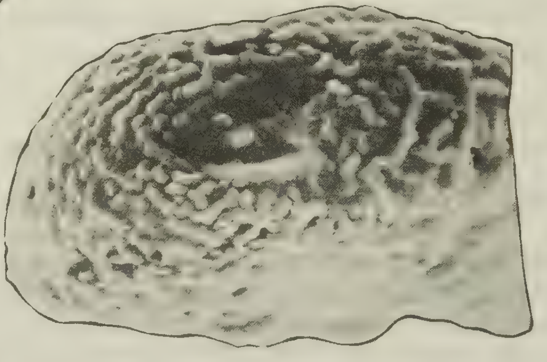
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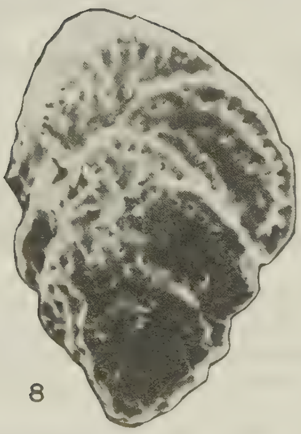
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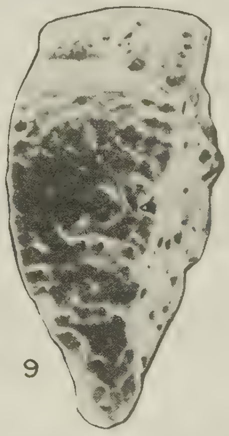
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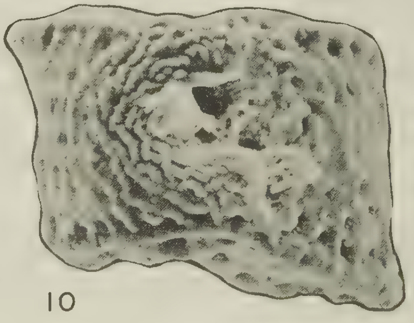
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Figs. 1-3 Bolivina variabilis (Williamson)
1, 2: Front views; 3: View of opening

Fig. 4 B. cf. difformis (Williamson)
Front view

Figs. 5-7 B. pseudoplicata Heron-Allen and Earland
5, 6: Front views; 7: View of opening

Figs. 8-10 B. rhomboidalis (Millett)
8: Front view; 9: Side view; 10: View of opening

Bolivina quadrata Cushman and McCulloch, 1942, p. 205, pl. 25, fig. 13-a,b.

Bolivina paula Bock, 1971, p. 46, pl. 16, fig. 15 (*non* Cushman and Cahill)

3.2 *Bolivina cf. difformis (Williamson)*

(See Fig. 4)

Textularia variabilis Williamson var. *difformis* Williamson, 1858, p. 77, pl. 6, fig. 166, 167.

Bolivina difformis Balkwill and Wright, 1885, p. 335. Cushman, 1922-b, p. 32, pl. 4, fig. 1; 1937, p. 164, pl. 15, fig. 13-17.

Bolivina cf. *difformis* (Williamson), Sellier de Civrieux, 1976, p. , lám. , fig.

Bolivina dilatata Goes (en parte), 1894, pl. 9, fig. 8-a,b, (*non* Reuss).

3.3 *Bolivina pseudoplicata Heron-Allen and Earland*

(See Figs. 5-7)

Bolivina pseudoplicata Heron-Allen and Earland, 1930, p. 81, pl. 3, fig. 36-40. Cushman, 1937, p. 166, pl. 19, fig. 12-20; 1944, p. 29, pl. 4, fig. 7, 8; 1949, p. 31, pl. 6, fig. 11, 12. Cushman and McCulloch, 1942, p. 204, pl. 25, fig. 4-7. Hoglund, 1947, p. 263, pl. 24, fig. 2; pl. 32, fig. 8-11, text-fig. 287. Voorthuysen, 1951, p. 24, pl. 1, fig. 28; 1960, p. 249, pl. 11; fig. 9. Parker, 1952-a. p. 414, pl. 5, fig. 17; 1952-b, p. 444, pl. 4, fig. 11. Walton, 1955, p. 1002, pl. 102, fig. 1. Todd and Bronnimann, 1957, p. 33, pl. 8, fig. 28. Todd and Low, 1961, p. 16, pl. 1, fig. 19. Haake, 1962, p. 39, pl. 2, fig. 19. Ayala-Castañares, 1963, p. 63, lám. 5, fig. 6. Sliter, 1970, p. 160, pl. 3, fig. 1-6; pl. 8, fig.12, 13. Murray, 1971, p. 107, pl. 43, fig. 1-7. Haynes, 1973, p. 132, pl. 10, fig. 3; pl. 11, fig. 7, text-fig. 25 (20, 21). Levy *et al.*, 1974, pl. 2, fig. 11, 15. Sellier de Civrieux, 1976, p. , lám. , fig.

Bolivina plicata H.B. Brady, 1870, p. 302, pl. 12, fig. 7-a, b. Goes, 1894, p. 51, pl. 9, fig. 487, 488 (*non* d'Orbigny).

Bolivina subexcavata Cushman and Wickenden, 1929, p. 9, pl. 4, fig. 4-a, b. Cushman, 1937, p. 138, pl. 18, fig. 33. Cushman and McCulloch, 1942, p. 214, lám. 27, fig. 3, 4. Heron-Allen and Earland, 1930, p. 81, pl. 3, fig. 36-40. Phileger and Ewing, 1962, pl. 5. Sliter, 1970, pl. 4, fig. 1-5; pl. 8, fig. 14.

Bolivina lowmani Bock, 1971, p. 46, pl. 16, fig. 14 (*non* Phleger and Parker).

3.4 *Bolivina rhomboidalis (Millett)*

(See figs. 8-10)

Textularia rhomboidalis Millett, 1899, p. 559, pl. 7, fig. 4. Sidebottom, 1905, p. 8, pl. 2, fig. 2.

Bolivina rhomboidalis (Millett) Cushman, 1922-b, p. 28; 1937, p. 138, pl. 18, fig. 7. Bermudez, 1935, p. 194. Hofker, 1964, p.77, figs. 205-206. Sellier de Civrieux, 1976, p. , lám. , fig.

3.5 *Bolivina tortuosa Brady*

(See Figs. 11-14)

Bolivina *tortuosa* Brady, 1884 (parte), p. 420; pl. 52. fig. 31-34. Egger, 1893, (parte), p. 292. Heron-Allen and Earland, 1911, p. 317, pl. 10, fig. 3, 4; 1913, p. 66, pl. 5, fig. 1. Cushman, 1922-a, p. 49, pl. 9, fig. 5. Cushman and McCulloch, 1942, p. 220, pl. 27, fig. 12-a,b. Todd and Bronnimann, 1957, p. 34, lám. 8, fig. 24. Hofker, 1951, p. 75, 76, fig. 39; 1956, p. 61, 62, 6 pl., fig. 22-29; 1964, p. 77, fig. 208. Sellier de Civrieux, 1976, p. , lám. , fig.

Bolivina *tortuosa* Brady var. *atlantica* Cushman, 1936, p. 57, pl. 8. fig. 8-a,b.

Sigmavirgulina *tortuosa* (Brady) Loeblich and Tappan, 1957, p. 227, pl. 73, fig. 1, 2.

3.6 *Bolivina torqueata Cushman and McCulloch*

(See Figs. 15-17)

Bolivina *torqueata* Cushman and McCulloch, 1942, p. 215, pl. 27, fig. 5,6. Sellier de Civrieux, 1976, p. , lám. , fig.

Bolivina *rhomboidalis* Bermudez and Seiglie, 1963, p. 25, lám. 19, fig. 4 (*non* Millett).

3.7 *Bolivina ortegaie Sellier de Civrieux*

(See Figs. 18-21)

Bolivina *ortegai* Sellier de Civrieux, 1976, p. , lám. , fig.

3.8 *Bolivina cf. compacta Sidebottom*

Bolivina *robusta* H.B. Brady var. *compacta* Sidebottom, 1905, p.15, pl. 3, fig. 7.

Bolivina *compacta* Sidebottom, Cushman, 1911, p. 36, text-fig. 58; 1921, p. 137, pl. 26, fig. 7; 1937, p. 135, pl. 17, fig. 22-24. Cushman and McCulloch, 1942, p. 190, pl. 23, fig. 4. Cushman and Todd, 1947-a. p. 18, pl. 3, fig. 5. Sliter, 1970, p. 157, pl. 1, fig. 1-5; pl. 8, fig. 4,5.

Bolivina cf. *compacta* Sellier de Civrieux, 1976, p. , lám. , fig.

Bolivina *variabilis* Todd and Bronnimann, 1957, p. 35, pl. 8, fig. 31.

3.9 *Bolivina Nairi Sellier de Civrieux*

(See Figs. 25-26)

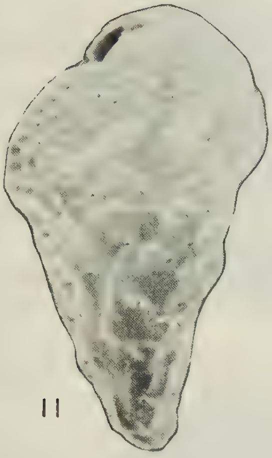
Bolivina *nairi* Sellier de Civrieux, 1976, p. , lám. , fig.

3.10 *Bolivina cf. lepida Sliter*

(See Fig. 27)

Bolivina *lepida* Sliter, 1969, p. 1, pl. 1, fig. 1-3; 1970, pl. 2, fig. 1-3; pl. 8, fig. 6-9.

Bolivina cf. *lepida* Sellier de Civrieux, 1976, p. , lám. , fig.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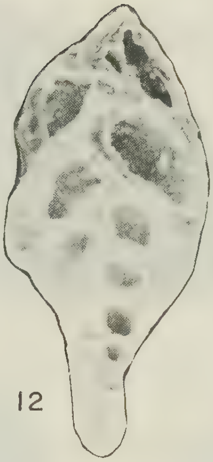
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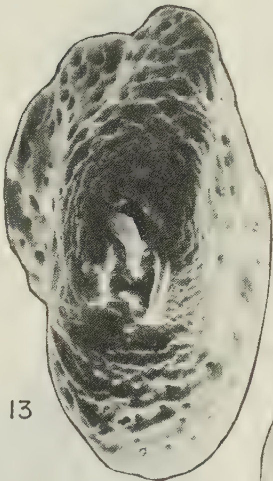
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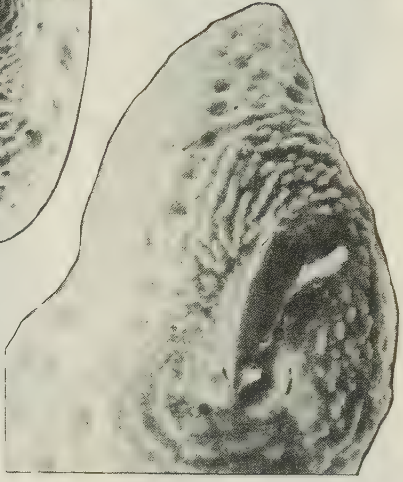
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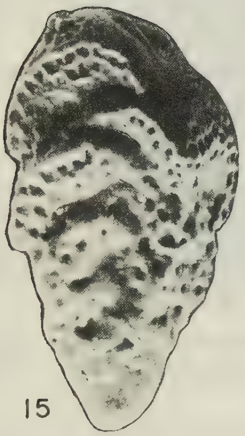
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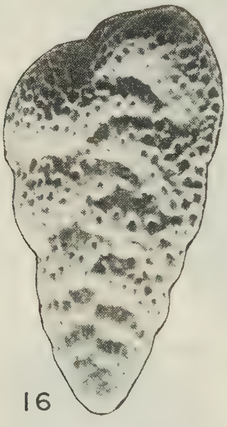
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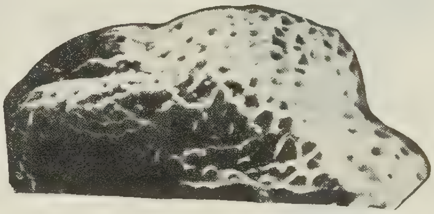
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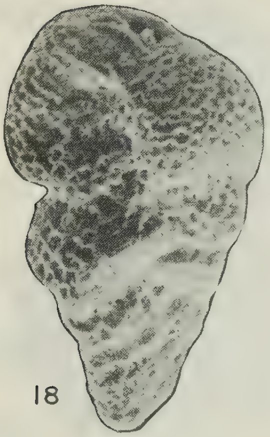
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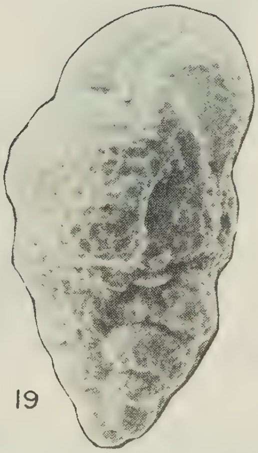
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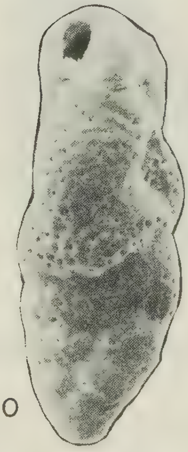
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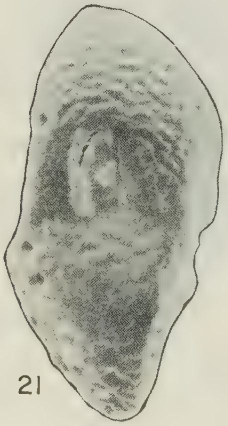
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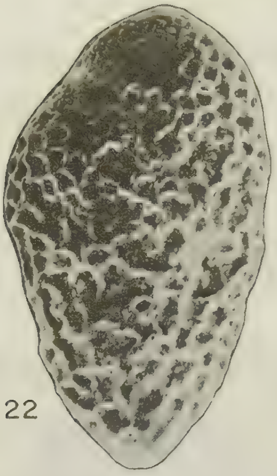
Figs. 11–14 B. tortuosa Brady
11: Front view; 12: Longitudinal section;
13,14: Views of opening

Figs. 18–21 B. ortegai Sellier de Civrieux
18: Front view; 19: Oblique longitudinal section
20: Side view; 21: View of opening



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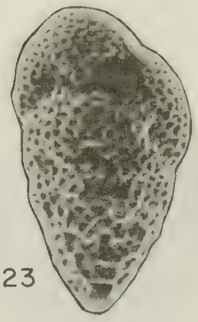

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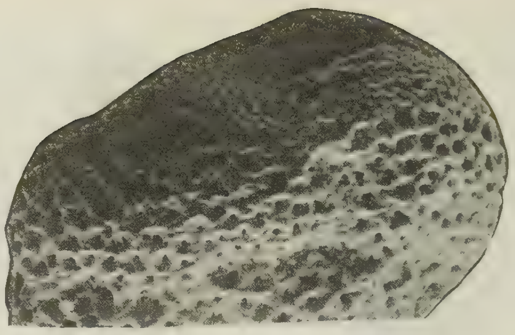

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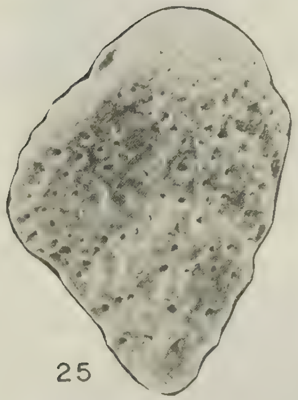

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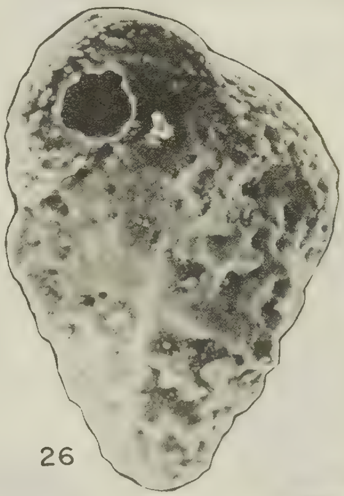

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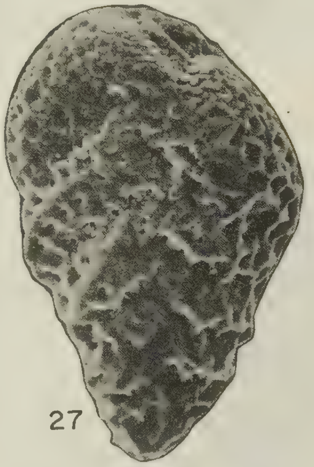

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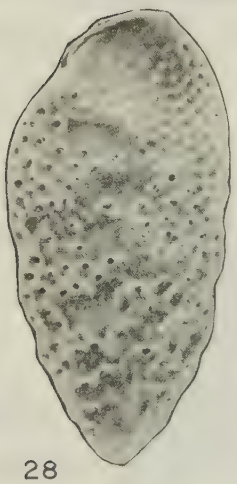

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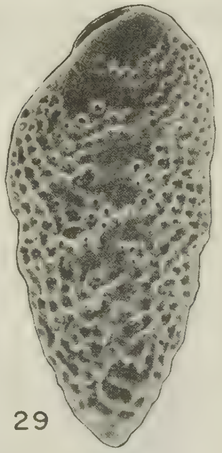

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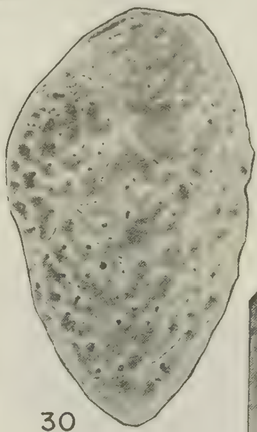

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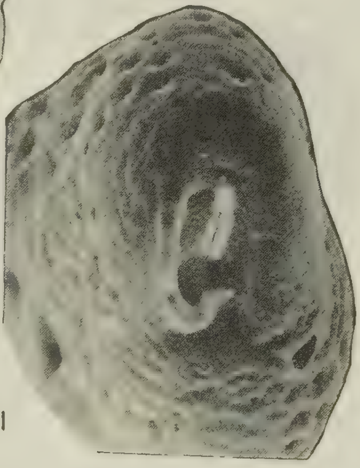

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Figs. 22-24 B. cf. compacta Sidebottom
22,23: Front views; 24: Detail of the opening

Figs. 25-26 B. nairi Sellier de Civrieux
Front views

Fig. 27 B. cf. lepida Sliter
Front view

Figs. 28-31 B. merecuanai Sellier de Civrieux
28-30: Front views; 31: View of opening

3.11 *Bolina merecuanai* Sellier de Civrieux

(See Figs. 28-31)

Bolivina merecuanai Sellier de Civrieux, 1976, p. , lám. , fig.

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ASPECTS OF THE ECOLOGY AND BIOGEOGRAPHY OF THE INTERTIDAL AND SHALLOW-WATER BALANOMORPH CIRRIPEDIA OF THE CARIBBEAN AND ADJACENT SEA-AREAS

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Abstract

Intertidal barnacles are poorly represented on open coast shores of the Caribbean, and the species diversity in the intertidal and shallow water habitats is lower than in the tropical eastern Pacific. The reduced cirripede fauna of the Caribbean can be explained by the different ecosystem and geological history of the region. Compared with the tropical eastern Pacific and nearby parts of the western Atlantic, the Caribbean has a smaller tidal range, a lower biomass of plankton, a greater development of coral reefs and more shores formed from porous reef limestones: these are all unfavourable to development of a barnacle zone. Intertidal grazing by reef fish and sea-urchins also reduces barnacle populations. The importance of the ecosystem, especially the reef biotype, is shown by better growths of barnacles in Caribbean harbours and bays where coral reefs are absent and the water richer in plankton and other particles, and by the reduced barnacle populations found on the offshore islands of the eastern Pacific where some coral reefs are present. A small number of species common to the Caribbean and the tropical eastern Pacific are apparently relicts of a once continuous shallow water fauna of Tertiary times, a fauna slowly modified by the tectonic movements and climatic changes during the formation of the present-day Caribbean and its complete separation from the eastern Pacific.

Resumen

En las costas del Mar Caribe escasean los cirrípedos litorales (balanus) típicos de las zonas de mareas, los cuales presentan en estos habitats una diversidad específica menor que en localidades similares del Pacífico oriental tropical. Para explicar la escasez de cirrípedos en el Caribe, hay que considerar las diferencias que existen en el ecosistema, así como la historia geológica de la región. Si se compara el Caribe con las zonas adyacentes inmediatas, respectivamente del Atlántico occidental y del Pacífico oriental tropical, se observa que en el Mar Caribe las mareas son más cortas, la biomasa planctónica es menor y los arrecifes de coral aparecen más desarrollados que en las otras regiones mencionadas, y además las costas del Caribe están formadas principalmente por rocas calizas porosas. Todas esas características no favorecen el desarrollo de las poblaciones de cirrípedos. Además hay que considerar la acción depredadora de los peces de arrecife y los erizos de mar, que contribuye a que disminuyan las poblaciones de esos crustáceos. La importancia del ecosistema, principalmente del biotipo de arrecife, aparece evidente al observar que los cirrípedos se desarrollan bién en los puertos y bahías del Caribe, en donde no existen arrecifes de coral, y tanto el plancton como las partículas orgánicas son abundantes, mientras que en las islas del Pacífico oriental, donde existen corales, las poblaciones de cirrípedos escasean. Solamente unas pocas especies de cirrípedos son comunes al Mar Caribe y el Pacífico oriental tropical, las cuales son probablemente reliquias de la fauna común que existía en las aguas someras de esa región durante la Era Terciaria. Esa fauna se ha ido modificando lentamente, con los movimientos tectónicos y los cambios climáticos concurrentes con la formación del Mar Caribe actual y su separación completa del Océano Pacífico.

1. INTRODUCTION

One of the best-known features of marine coastal life is the almost universally developed zone of acorn barnacles found between high and low levels of ordinary tides. This zone is often used as a major reference point in describing rocky shore zonation patterns, and the recent compilation of the late Professor T.A. Stephenson's researches (Stephenson and Stephenson, 1972) shows how worldwide it usually is. On Caribbean shores, however, this barnacle zone is always much less obvious compared with shores of nearby tropical seas, e.g., the eastern Pacific and the north-east coast of Brazil. Fairly dense communities of barnacles can be found in the Caribbean in harbours and in the sublittoral but, even then, the number of species seems to be less than in the tropical eastern Pacific. Our studies suggest a number of reasons, both ecological and biogeographical, for this lack of development of barnacle populations in the Caribbean, but before discussing these we shall examine the problem in a little more detail.

2. CARIBBEAN AND PACIFIC COASTS COMPARED

Let us look at a typical Caribbean rocky shore community, such as is found on many open coasts exposed to a moderate degree of wave-action and where the range of tide is usually less than a metre. Most commonly the rock will be calcareous, derived from reef debris in varying degrees of consolidation, though, of course, volcanic and older sedimentary rocks do form the shore in places. The typical beach rock is porous, much eroded and usually forms gently sloping platforms. Quite often there is no real zone of barnacles in such places; sometimes a few individuals will be found in cryptic positions under overhangs, or there might be a more obvious barnacle population on the harder lumps of rock or at certain places on the platforms. When a population of barnacles does develop, the zone is often only a few decimetres in vertical width, and is composed usually of two dominant species; *Chthamalus angustitergum* and *Tetraclita stalactifera*. Sometimes only the *Tetraclita* grows on the coral rock; the *Chthamalus* then occurs on its shell. Where conditions are locally suitable these two species can be found all over the Caribbean but, in wave-swept places, they are accompanied by two surf-loving species *Catophragmus imbricatus* and *Newmanella radiata*, which sometimes replace them.

A much more evident barnacle community may develop in sheltered Caribbean bays and harbours, but then the species composition changes (Southward, 1975). With increasing shelter from waves, *Chthamalus angustitergum* is progressively replaced by *C. fissus* and the more characteristic harbour barnacles, such as *Balanus amphitrite*, *B. reticulatus*, *B. eburneus* and *B. assimilis*, take over the lower levels. These species may also be found in the sublittoral together with *B. trigonus* and *Megabalanus antillensis*, the latter species also being found at low tide levels on surf-washed shores. The widely distributed euryhaline species *Balanus pallidus* can occur in brackish waters but, except for Lake Maracaibo, parts of Trinidad and the Panama Canal, many of the Caribbean records for this species could be due to washed-up specimens drifted from the Orinoco and Amazon low-salinity complexes (Bacon, 1976).

In contrast, let us examine a rocky shore of the tropical eastern Pacific, such as can be found along the Pacific coast of Panama, but a short distance across the Isthmus from typical Caribbean conditions on the Atlantic side. The shores here are typically of harder rock, primarily volcanic, and calcareous sediments are much less evident, being confined to the offshore islands. The barnacle communities are quite obvious and occupy a large section of the much wider intertidal zone resulting from the greater amplitude of the tides, which often exceed 6 m. Dense populations of several species cover black volcanic rocks exposed to the sun, very different from the situation usually observed in the Caribbean. There is a distinct 'splash' zone high up the shore, formed by the chthamalid *Euraphia imperatrix*; this occupies a position comparable with that of its relative *E. depressus*, found in the Mediterranean (Southward, 1964) and, like the latter, it must be very resistant to heat and desiccation (cf. Monterosso, 1933). The normal barnacle zone consists of several other species; in the upper half of the midlittoral there is a dense community of a *Chthamalus*, once thought to be an endemic species (*C. panamensis*) but now regarded as *C. fissus*, and apparently also identical with the species found in sheltered waters in the Caribbean. The lower half of the main barnacle zone is usually dominated by *Balanus inexpectatus* in more turbid situations, and *Tetraclita panamensis* (cf. Reimer, 1976) plus *Catophragmus pilsbryi* in more wave-beaten places, sometimes all together. At low tide, and in the sublittoral, many other species of barnacles may be found; *Balanus pacificus*, *B. trigonus*, *B. glyptopoma* subspecies, *Megabalanus coccopoma* and *M. vinaceus*. *Tetrabalanus polygenus*, a *Euraphia* species (possibly *rhizophorae*) and *B. peruvianus* are common in brackish waters where mangroves are present. In harbours, *B. trigonus* is accompanied by *B. eburneus* and *B. assimilis*, while *B. pallidus* occurs in the brackish water of the locks on the Pacific side of the Panama Canal.

Table I lists all the common balanomorph barnacles, other than the epizoic and coral-inhabiting types, reported from the Caribbean and adjacent sea areas; they can be classified into four main groups according to their geographical range. Six species are cosmopolitan, and are found in most tropical seas; *B. amphitrite*, *B. eburneus*, *B. pallidus*, *B. reticulatus*, *B. trigonus*, *B. venustus*, possibly also *M. coccopoma*. Four are endemic to the Neotropical Region; *B. assimilis*, *Tetraclita stalactifera*, *Chthamalus fissus*, and the mangrove-dwelling *Euraphia rhizophorae*. Six species appear to be found only on the Caribbean side and not in the eastern Pacific; *Catophragmus imbricatus*, *Chthamalus angustitergum*, *Tetraclitella divisa*, *Newmanella radiata*, *Megabalanus antillensis* (the latter two also found in Brazil) and, possibly, *B. subalbidus*, which is much commoner in south-eastern U.S.A. At least 10 species appear to be endemic to the tropical eastern Pacific. After excluding fossils and species which are not found in the Caribbean proper, or in the fully tropical region of the eastern Pacific, we are left with a total of 59% endemic to one side or the other of the Isthmus, 15% found on both sides and only 26% cosmopolitan tropical. The endemics comprise 35% of the species in the Caribbean and 48% of the species in the tropical eastern Pacific; there is thus little doubt that the species diversity is relatively lower in the Caribbean. However, it is important to note that there is also a lower diversity of shore barnacles on the coralliferous offshore islands in the Gulfs of Panama and Chiriqui.

The apparent reasons why the Caribbean has a reduced barnacle fauna can be grouped under two headings: (a) the present differences in the ecosystem compared with the tropical eastern Pacific; (b) the geological history of the area and its effects on the evolution and dispersal of the barnacles.

3. ECOLOGICAL FACTORS

The shallow-water ecosystem of the Caribbean is, undoubtedly, different from that of neighbouring seas (e.g., Glynn, 1972; see also other contributions to the Symposium on Panamic Biota, ed. Jones, 1972; Dana, 1975, 1976; Millman, 1973). The following factors would be expected to have markedly unfavourable effects on intertidal barnacle communities and on some sublittoral species: (1) the widespread beachrock, derived from developing or fossil reef limestone, is not a favourable substratum for Balanomorph Cirripedia. The surface often erodes rapidly and the porosity leads to desiccation of the tissues in those species with a membranous basis; the growing reefs themselves are unsuitable for settlement of all but the coral-inhabiting barnacles, not discussed here; (2) the small tidal range, and consequent narrow zone suitable for settlement of intertidal species, reduces the overall population in a given locality; if the planktonic larval stages are much dispersed by currents (as is normal) there might be times when the numbers returning to settle will not be sufficient to maintain the population. Thus the barnacle zone could vary from year to year, and the smaller islands must for the most part, depend on larvae brought in from other places by currents; (3) the clear blue-water and low standing crop of plankton, without marked seasonal fluctuations (cf. Cushing, 1959; Menzel and Ryther, 1961), means that the larval stages will always have greater difficulties in finding food than those in other sea areas, and hence may be more dependent on local conditions to produce occasional favourable settlement.

The effects of all these factors would be expected to prevent development of a normal, densely populated barnacle zone; but there is a further factor which could be equally important, namely the ability of sublittoral sea-urchins and reef fish from nearby coral reefs

TABLE I

Common Balanomorph Cirripedia of the Caribbean and adjacent seas, omitting epizoic forms and the coral barnacles

	Geographical Range						
Species	Caribbean region	Gulf of Mexico	Southeast U.S.A.	Northeast Brazil	Eastern Tropical Pacific and/or Gulf of California	Cosmopolitan tropical and/or subtropical	
Catophragmus imbricatus Sowerby	+	–	–	–	–	–	Tropical Western Atlantic
Tetraclitella divisa (Nilsson-Cantell)	+	–	–	–	–	–	
Newmanella radiata (Brugière)							
b/(Balanus glyptopoma glyptopoma Pilsbry)	+	+	–	–	–	–	
Chthamalus angustitergum Pilsbry	+	–	+	–	–	–	
Tetraclita stalactifera Lamarck	+	–	+	–	–	–	
(Chthamalus fragilis Darwin)	–	+	+	–	–	–	
a/(Balanus pacificus prebrevicalcar Ross)	–	–	+	–	–	–	
Balanus subalbidus Henry	+	+	+	–	–	–	
Megabalanus antillensis (Pilsbry)	+	–	+	+	–	–	
b/Chthamalus fissus Darwin	+	+	–	+	+	–	Tropical Americas
b/Balanus assimilis Darwin	+	–	+	+	+	?–	
b/Euraphia rhizophorae (de Oliveira)	+	–	–	+	+	–	
Balanus reticulatus Utinomi	+	–	+	+	–	+	Cosmopolitan
Balanus pallidus Darwin	+	–	–	+	+	+	
Balanus venustus Darwin	+	+	+	+	–	+	
Balanus amphitrite amphitrite Darwin	+	+	+	+	+	+	
Balanus eburneus Gould	+	+	+	+	+	+	
Balanus trigonus Darwin	+	+	+	+	+	+	
Megabalanus coccopoma (Darwin)	–	–	–	?+	+	–	
b/Catophragmus pilsbryi Broch	–	–	–	–	+	–	Tropical Eastern Pacific
Euraphia imperatrix (Pilsbry)	–	–	–	–	+	–	
Tetraclita stalactifera confinis Pilsbry	–	–	–	–	+	–	
b/Tetraclita panamensis Pilsbry	–	–	–	–	+	–	
b/Balanus glyptopoma eyerdami Henry	–	–	–	–	+	–	
b/Balanus glyptopoma panamensis Rodgers	–	–	–	–	+	–	
Balanus inexpectatus Pilsbry	–	–	–	–	+	–	
b/Balanus pacificus pacificus Pilsbry	–	–	–	–	+	–	
b/Balanus pacificus mexicanus Henry	–	–	–	–	+	–	
Tetrabalanus polygenus Cornwall	–	–	–	–	+	–	
Megabalanus peninsularis (Pilsbry)	–	–	–	–	+	–	
Megabalanus spp.	–	–	–	–	+	–	
Megabalanus vinaceus (Darwin)	–	–	–	–	+	–	

Extinct

Species marked represent taxonomic changes; systematic evidence will be presented in a later contribution. The rest of the systematics follows the revision by Newman and Ross (1976)

Species in brackets are not used in calculating percentage of endemics to graze over the intertidal zone where the inshore waters are clear and of full salinity (Newman, 1960). The tooth-marks left by these grazers on typical Caribbean coral rock are commonly seen and, in places where, for example, the sea-urchin Diadema is locally abundant, intertidal cirripedes may be absent or confined to underhanging surfaces and crevices too small to admit the predator. Often, on outlying wave-washed cays or reefs, places where, in other seas, a good barnacle zone might be expected, predation might be so strong that the only cirripede present intertidally is Lithotrya, a pedunculate form which lives in burrows in coral rock. This sort of predation could well operate in other tropical areas with extensive reef development but, in the Caribbean,it must reinforce the other local adverse factors. Taken together, all these factors provide a convincing explanation why the barnacle zone of open coast shores in the Caribbean is so much less obvious than on the Pacific coast of Central America, where tides are of greater amplitude, coral reefs less developed and the plankton biomass much higher, The presence of a better barnacle population in many Caribbean harbours and creeks reinforces this view of the role of the ecosystem since it would be expected that the richly organic environment of the partly enclosed bodies of water would assist breeding and settlement, while coral-reef grazers would be excluded. Conversely, the lower diversity and abundance of barnacles on the offshore islands in the Gulf of Panama and the Gulf of Chiriqui, where modest coral reefs exist, emphasizes the unfavourable character of the reef biotope rather than factors such as tidal range and insolation. Such evidence would tend to exclude thermal tolerance as being a primary deterrent to the existence of large numbers of intertidal barnacles on sun-exposed tropical shores, as suggested by Foster (1974).

4. BIOGEOGRAPHICAL IMPLICATIONS

It remains for us to determine how the distribution of the endemic species is related to the difference in ecosystems or if the present distribution has been influenced by the way in which the Caribbean has evolved in geological history (see reviews by Nagle, 1971; Uchupi, 1973; Maresch, 1974). According to present concepts of plate tectonics the Caribbean might have been derived from the Pacific (Dietz and Holden, 1970, 1972; Edgar, Ewing and Hennion, 1971; Malfait and Dinkelmann, 1972), or from new sea-floor formed at the same time as the opening up of the Atlantic (Santamaria and Schubert, 1974). Some geologists can find no evidence for large-scale movements and regard the Caribbean as an ancient ocean basin (Meyerhoff and Meyerhoff, 1972); it is true that there is uncertainty as to how much lateral shear has taken place along the fault lines or how much subduction has occurred where the plates meet (Beets, 1975; Silver, Case and Macgillavry, 1975; Peter, 1976; del Castillo, 1976). However, the existence of 'bridges' between continents, or of Continental Drift (Wegener, 1924) is an early and necessary concept in biogeography, long recognized as important in the Caribbean region and S. America (for an early discussion see Macbride, 1916). The Hypothesis of plate tectonics has provided a firm basis for biogeographical thinking (Smith, Briden and Drewry, 1973), and helps to explain present and past patterns of dispersal of several groups of terrestrial and shallow-water marine organisms (Valentine, 1971; Hallam, 1973; Tedford, 1974; Rosen, 1975; Foin, 1976).

There is much to recommend the view that a large part of the present Caribbean seafloor is an intrusion from the Pacific, a process that began in Jurassic times (refs. quoted above). On this hypothesis, the Antillean arc, or its precursor the Aves ridge, originally constituted a chain of islands joining the, then, continents of North and South America, at one time part of single tectonic plate. After the split of the American plate by the intrusion of the Pacific, and the eastward displacement of the Antilles, a new group of islands was uplifted near the site of the present Isthmus in the early Oligocene. Development of the new island chain and its ultimate joining together in the late Pliocene or early Pleistocene (Briggs, 1967; Keigwin, 1976) finally closed off the Caribbean from the eastern Pacific.

Presumably during the formation of the Caribbean and its separation from the Pacific there was a fairly gradual transition from the larger tidal amplitudes of the Pacific to the smaller tidal oscillations tuned to the size of the present Caribbean basin (Marmer, 1926), as the gaps across the Isthmus became narrowed. In considering the reaction of the earlier cirripede fauna to these changes, it must be remembered that the majority of the sessile balanomorph Cirripedia are tied to the shore and the immediate sublittoral, and hence their distributions may show features resembling those of terrestrial organisms rather than the pelagic life of the ocean and the benthos of deeper waters. Of the species listed (Table I), two appear to be genuinely amphi-american in distribution; *Chthamalus fissus*, including the former *C. panamensis*, is abundant along the Pacific coast from southern California through Panama to Peru, is less common in the Gulf of Mexico and, in the Caribbean, is restricted to harbours and other sheltered waters where the ecosystems are richer than along the open coast (Fig. 3). It is, presumably, a survivor of a former common intertidal fauna, originally widely distributed across the site of the present Caribbean. In contrast, the second, *Tetraclita stalactifera*, is most abundant and widely distributed in the Caribbean today, and also occurs in the extreme southeast of the U.S.A. and in northeast Brazil, regions with a recognizable tropical marine biota (Briggs, 1974) (Fig. 4). On the Pacific coast it is represented by a restricted population of the closely related "subspecies", *T. s. confinis*, which ranges from the Gulf of California to mid-Mexico. Apparently we have here a species which began adapting to life in the tropical Americas in the mid-Tertiary, after movement of the Antillean arc, and which managed to survive on this region of the Pacific coast. The restriction of the Pacific population might have resulted from the arrival of *T. panamensis*, or its ancestor, from the Indo-Pacific, after closure of the Isthmus (Fig. 4).

Many of the other species of barnacles common to the Caribbean and the eastern Pacific are cosmopolitan forms widely distributed in the tropics and subtropics; most of them are also harbour, or 'fouling', or brackish water tolerant, and it is, today, difficult to distinguish their true geographical affinities after several centuries of dispersal by ships. However, two further species may be amphi-american; one of these is *Euraphia rhizophorae*, but its specialized habitat on the roots of mangroves means that we may not yet have full details of its distribution. The other is *B. assimilis*, formerly regarded as a variety or subspecies of *B. improvisus*, but here classed as a full species. This form existed on both sides of S. America at the time of the BEAGLE voyage (1834) to judge from material in the Darwin collections in London and Cambridge and, today, it is commonest in the Caribbean in places where the ecosystem also favours survival of *Chthamalus fissus*, itself amphi-american.

More than half the species in Table I are local endemics, restricted either to the Caribbean and the tropical western Atlantic or to the tropical eastern Pacific (see examples, Figs. 1,2 and 3). How many of these have evolved since closure of the Isthmus, and how many have failed to survive on one side or the other due to the change in the ecosystem? We know that two of them, *B. glyptopoma* and *B. pacificus*, once occurred in places that now form part of the Caribbean, since fossils have been found in late Tertiary deposits in eastern Mexico and Panama (and also in Virginia) whereas the surviving subspecies are found along the Pacific coast only. However, the first species belongs to the "concavus" group of *Balanus*, which underwent almost worldwide extinction, and it is not presently possible to say what it is about Caribbean conditions, much less those elsewhere in the world, which were especially unfavourable. However, there has been a general shrinking in range, and extinction of Caribbean species, including molluscs, corals and coral-inhabiting barnacles, since the mid-Miocene (Nicol, 1961; Newell, 1971; Newman and Ladd, 1974). The restriction of tropical species is well illustrated by the present relictual distribution of *Catophragmus* (Fig. 7), the oldest and most generalized of the balanomorph barnacles. For other species, such as the Indo-Pacific originated forms of *Tetraclita* and *Megabalanus* (Fig. 6), the land barrier formed by the Isthmus might be sufficient reason for their restriction to the Pacific side. But other local endemics would seem to have evolved to suit the changed ecosystem; *Newmanella radiata* (Fig. 1) has a limited distribution strongly suggestive of southern Caribbean origins while *C. fragilis* might well have evolved from *C. fissus* to fit conditions in southeast U.S.A. *C. angustitergum* (Fig. 2) seems to be pre-eminently a Caribbean species and, perhaps, derived from some Atlantic ancestor. *Balanus subalbidus* could well be another local form evolved in the bayou conditions in southeast U.S.A.; possibly it was later replaced in all but a few specialized habitats by *B. improvisus*, introduced with shellfish from the Old World.

No doubt we shall never unravel fully the complications due to artificial introductions of shallow-water marine life, conscious or otherwise, but we can perhaps make a few deductions about the possible consequences to the barnacle faunas of a sea-level canal across Central

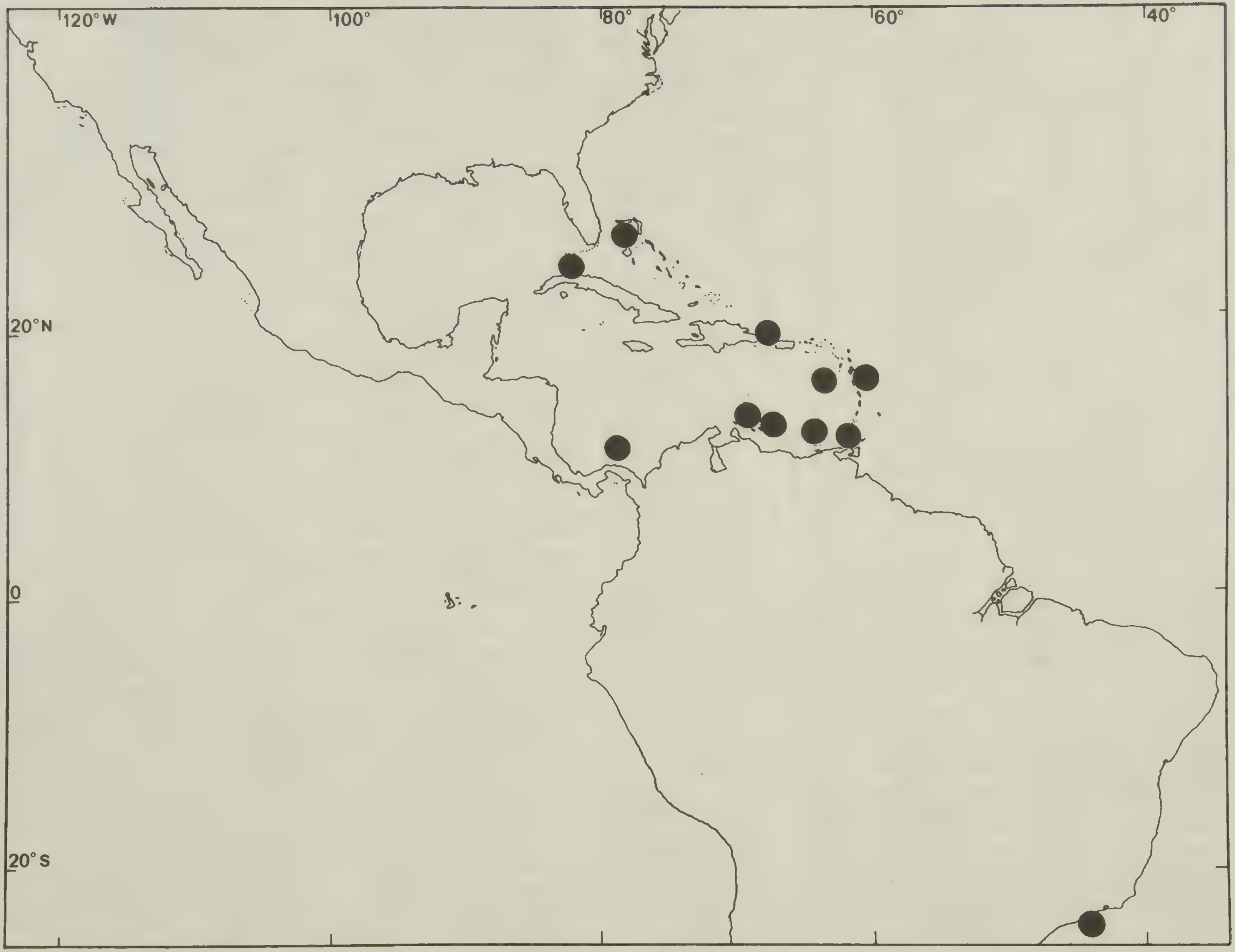
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Fig. 1 *Newmanella radiata* (Bruguière), endemic to the Caribbean and part of the tropical West Atlantic

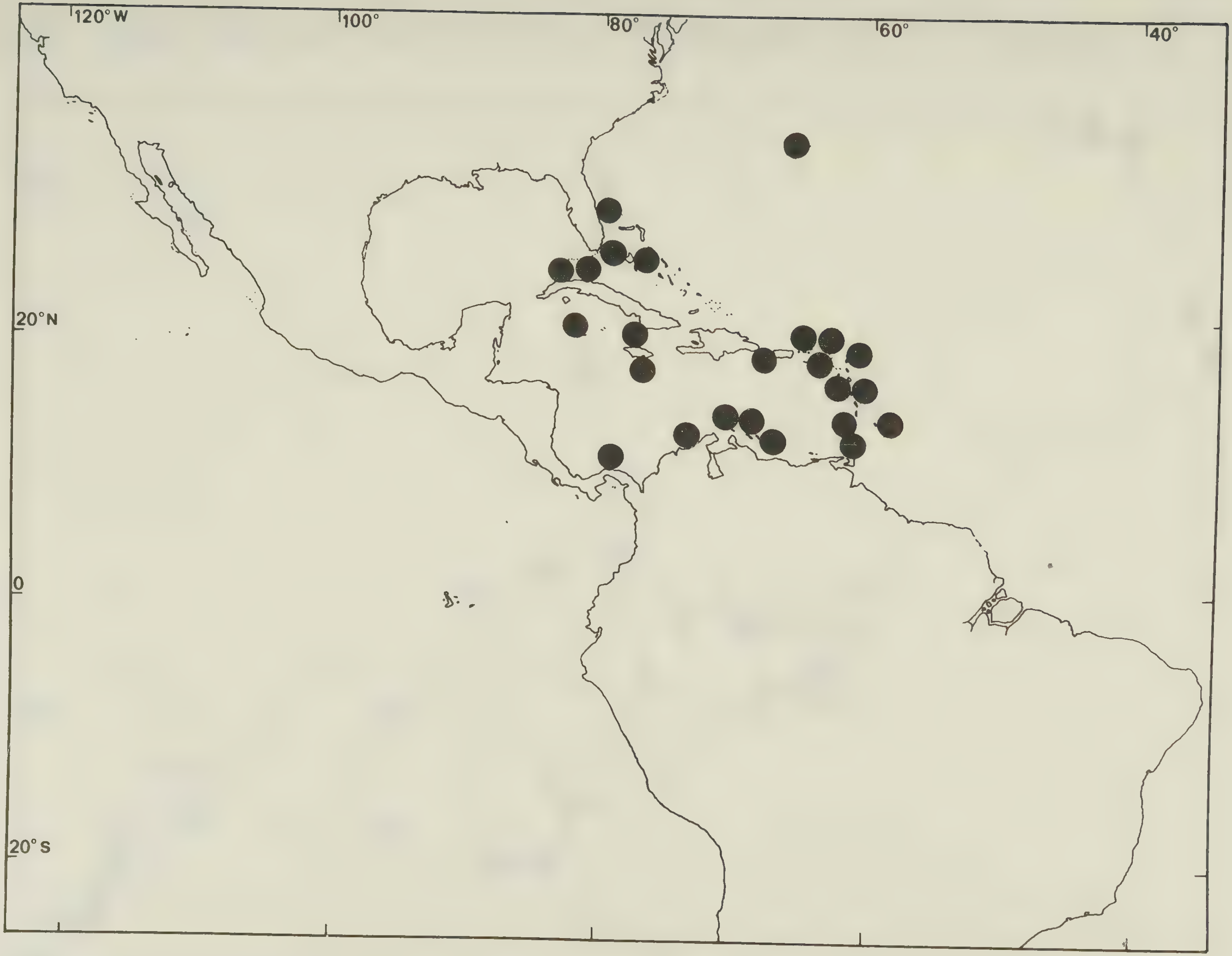
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Fig. 2 *Chthamalus angustitergum* Pilsbry, apparently endemic to the Caribbean only, but with an isolated outlying population in Bermuda

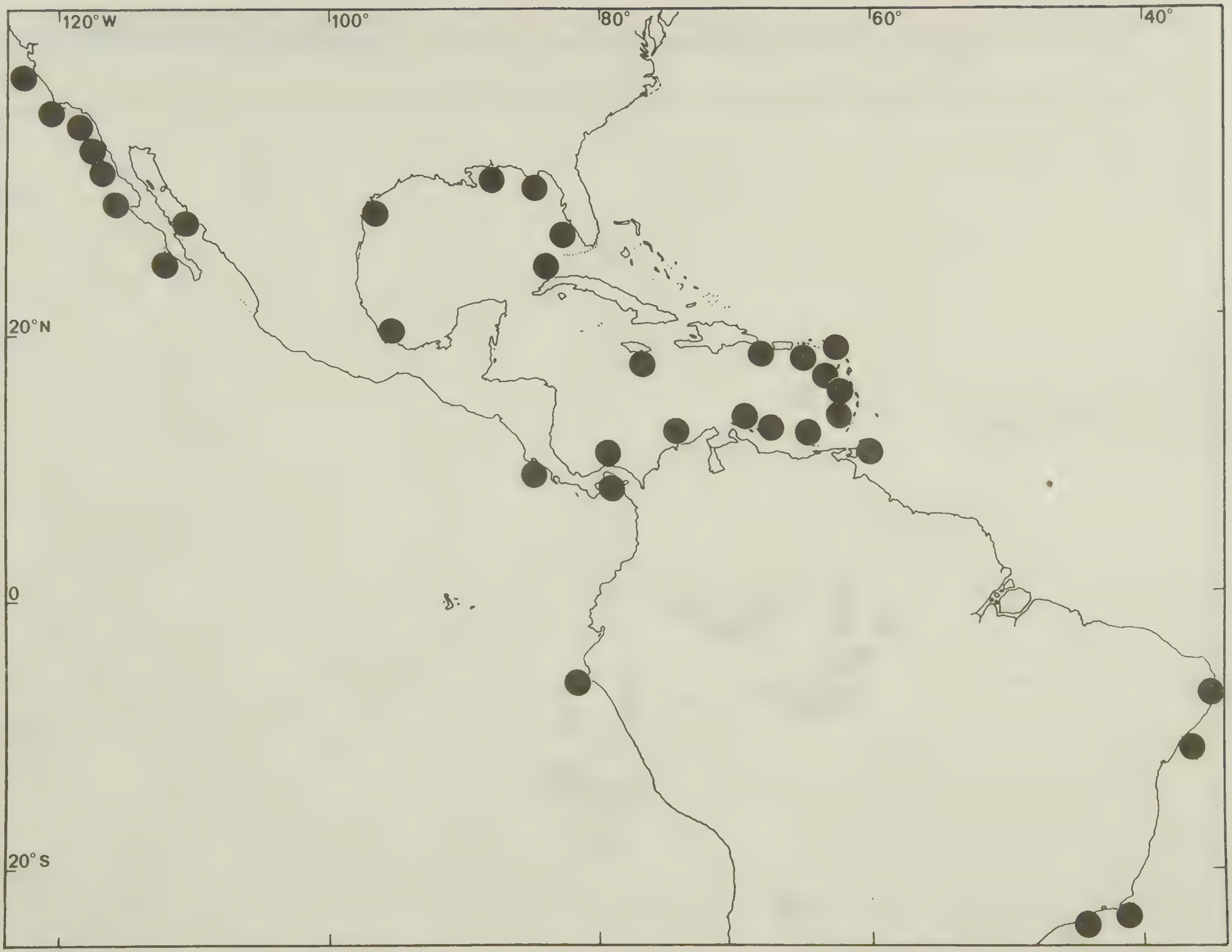
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Fig. 3 *Chthamalus fissus* Darwin, taken here to include also *C. panamensis* Pilsbry and *C. bisinuatus* Pilsbry of Southward 1975. This now enlarged species is apparently truly amphiamerican in distribution

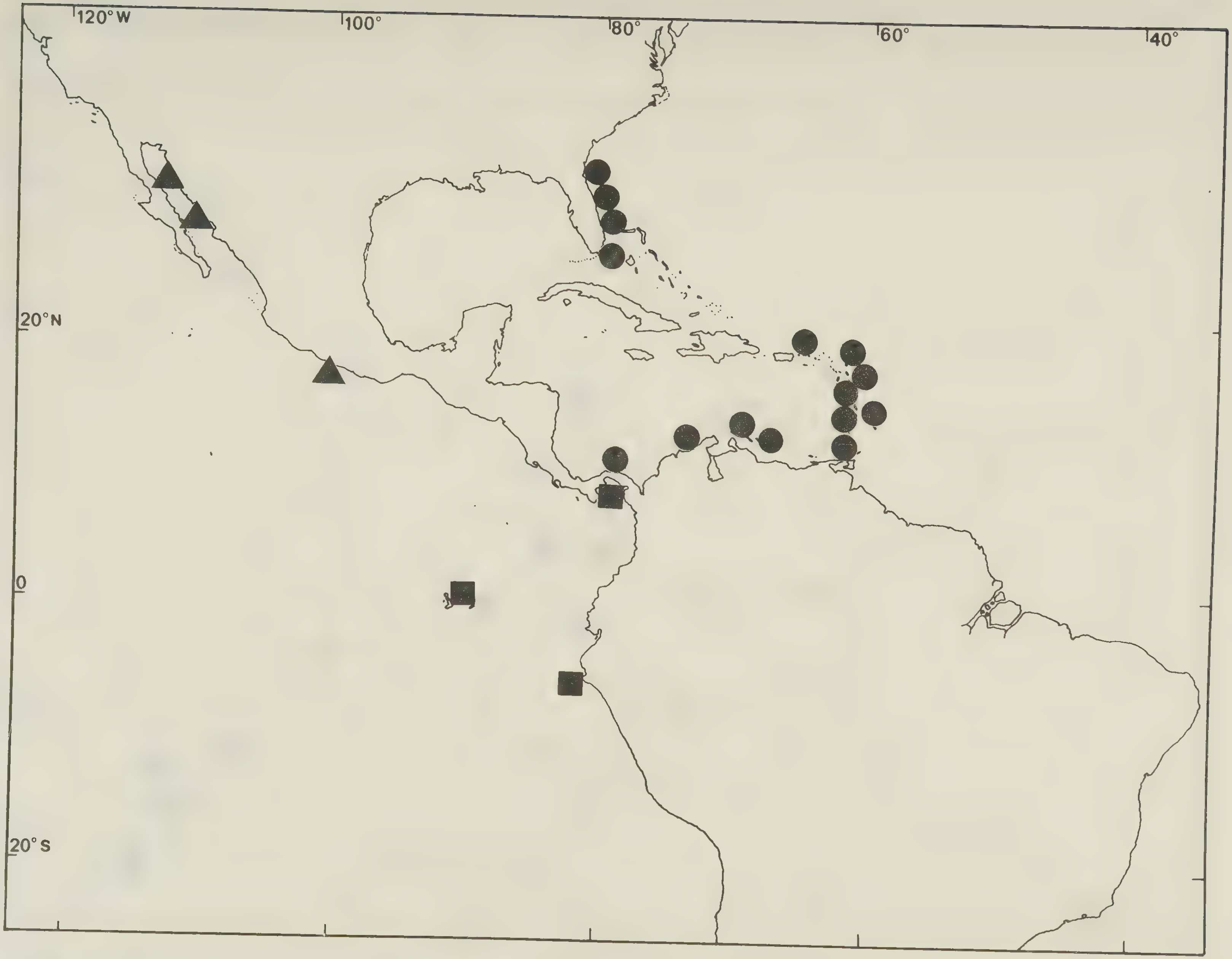
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Fig. 4 ● *Tetraclita stalactifera* (Lamarck); ▲ its relative on the Pacific coast, *T. stalactifera confinis* Pilsbry; and ■ *T. panamensis* Pilsbry, possibly of Indo-Pacific origin

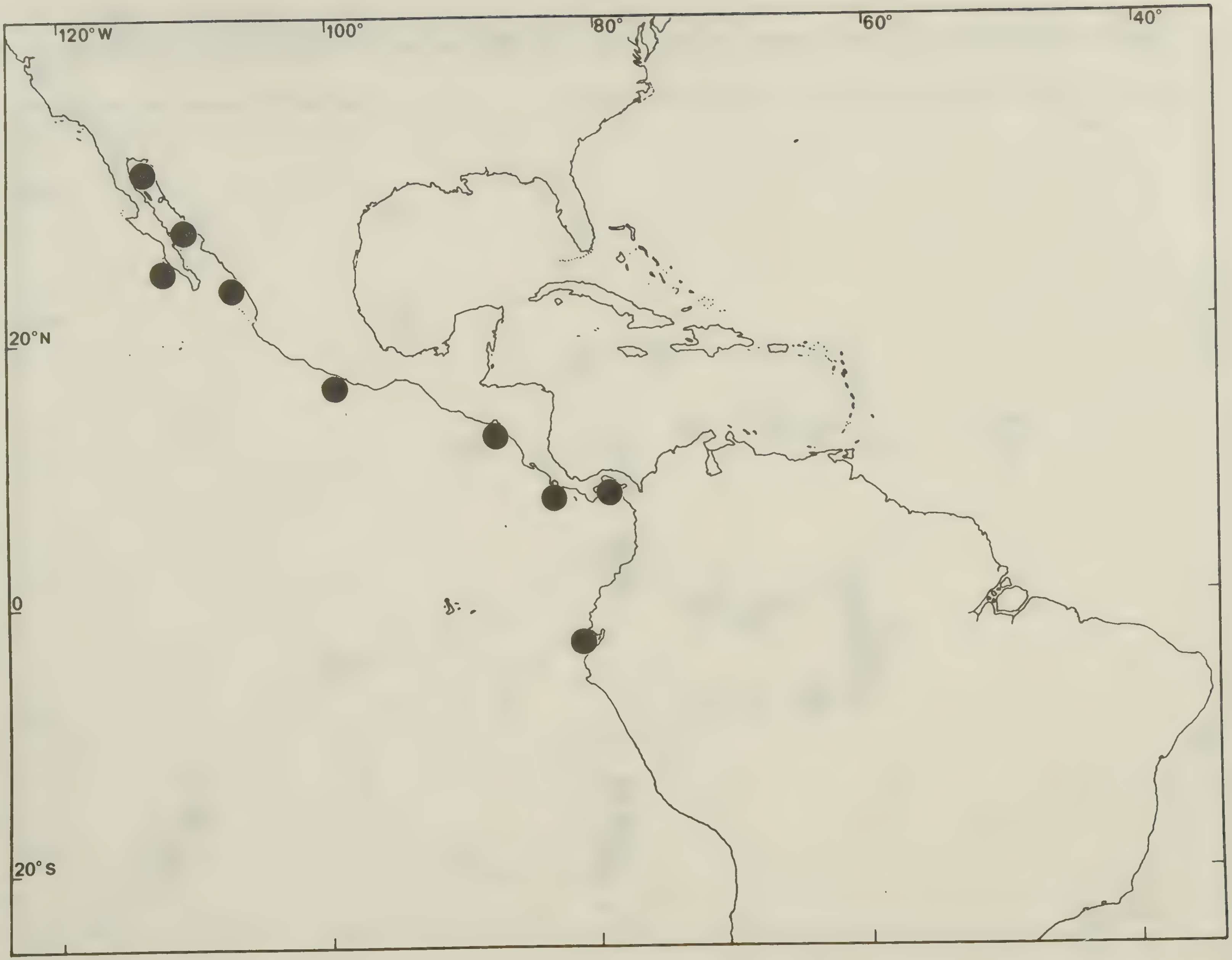
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Fig. 5 *Balanus inexpectatus* Pilsbry, endemic to the tropical eastern Pacific and the Gulf of California

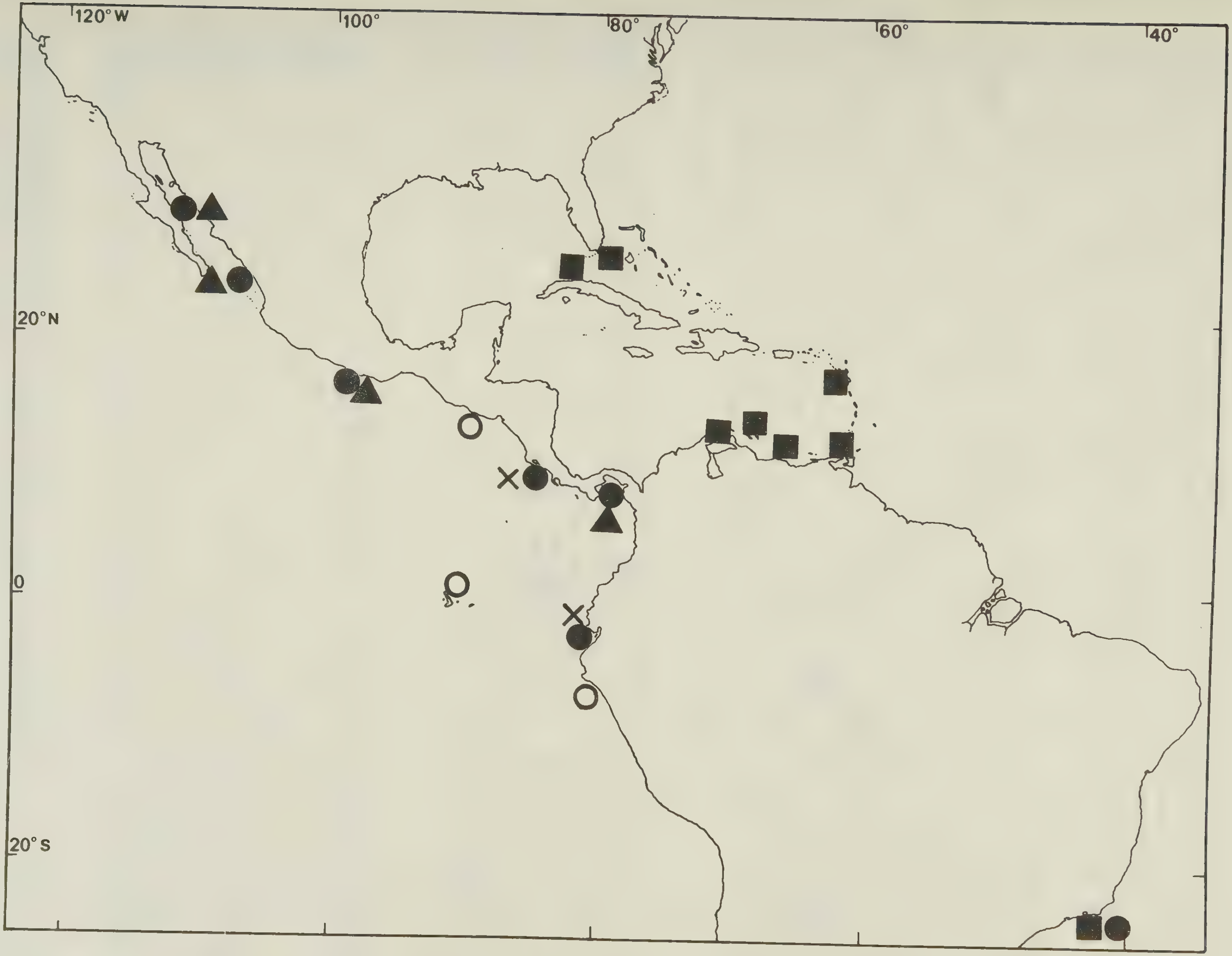

Fig. 6 ■ *Megabalanus antillensis* (Pilsbry), found in the Caribbean and parts of the tropical West Atlantic; ● *M. coccopoma* (Darwin), of uncertain distribution, but possibly once endemic to the tropical eastern Pacific; ▲ *M. peninsularis* (Pilsbry), endemic to the eastern Pacific; × *M. vinaceus* (Darwin); and ○ *Megabalanus* spp. undescribed. This genus provides an example of the greater species diversity of the eastern Pacific.

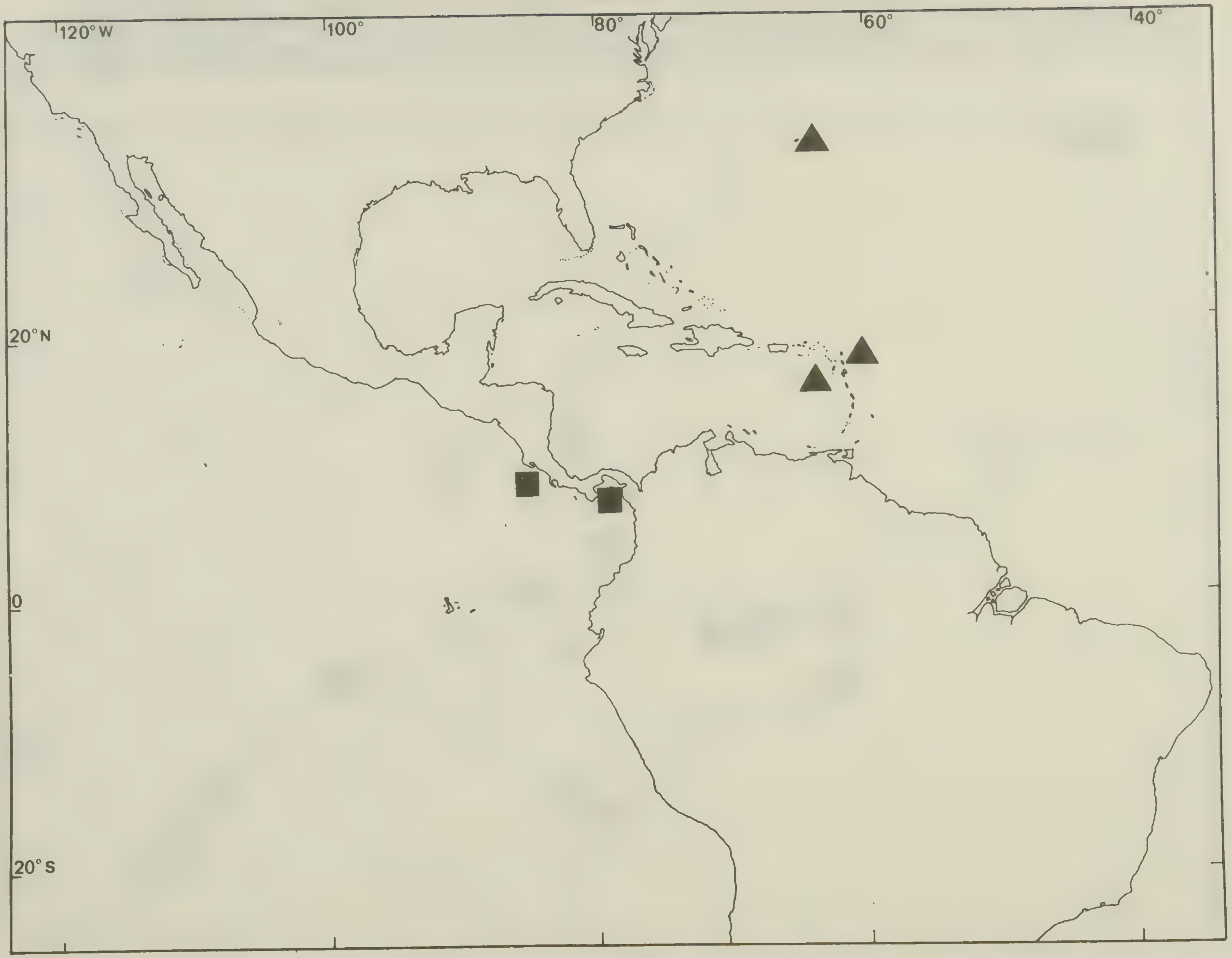

Fig. 7 ▲ Catophragmus imbricatus Sowerby, found in Bermuda, Antigua and Aves Island; ■ Catophragmus pilsbryi Broch, found on offshore islands along the Pacific coast of Costa Rica and Panama. These species appear to be relicts of a former widespread tropical group, now reduced to insular refuges.

America. As we have shown, there are some common elements, some of them relicts of a once continuous shallow water fauna, illustrating that the present differences in the ecosystems are not completely and mutually exclusive. But the larger number of species that are locally endemic proves that geographical separation, followed by distinctiveness of ecosystems, produced immense changes in the cirripede fauna. The same appears to be true for the shallow-water marine fish and molluscs (Rosenblatt, 1967; Houbrick, 1968) though, for the echinoderms, except possibly Acanthaster, the degree of present separation seems to depend on how the species level is defined (Chesher, 1972).

Much controversy exists among marine biologists as to the possible consequences of reopening communication between the eastern Pacific and the Caribbean (cf. Briggs, 1969 and Voss, 1972). Attitudes depend especially on the systematic level at which endemicity is recognized and on the apparent relationship with the two ecosystems. For shallow water fish, the fresh water barrier provided by Lake Gatun, in the present Panama Canal (Jones and Dawson, 1973) appears to have been successful in preventing transfer of all but the most euryhaline species (McCosker and Dawson, 1975). Among the balanomorph Cirripedia, the only two species likely to have been transferred on ships through the Canal are Balanus pallidus and B. eburneus. At present the former is only sporadically distributed on the Caribbean side and appears to be confined largely to the Canal system on the Pacific side. The latter species is widespread in the Western Atlantic but is known by a few scattered populations in the eastern Pacific and elsewhere. Removal of the fresh water barrier would probably lead to greater equalization of the fouling species in suitable habitats, but changes in the present Caribbean barnacle fauna, with its apparently specialized endemic elements, could probably take place gradually, with a general readjustment of reef communities.

5. CONCLUSIONS

Until recently little had been published on the systematics and distribution of the common balanomorph Cirripedia of the Caribbean and nearby seas, the only general study being that of Pilsbry (1916) as part of his monograph of the American species, New ecological and systematic investigations were begun by the Netherlands Antilles Study Group in the 1920s (Pilsbry, 1927; Nilsson-Cantell, 1933, 1939) and the collections built up by Dr. P. Wagenaar Hummelinck constitute the most comprehensive series yet. In the past few years further interest has been stimulated by expeditions and local studies (Ross, 1969; Bacon, 1976) and by the CICAR programme (Southward, 1975). Interest in the eastern Pacific revived earlier (Henry, 1941. 1943, 1960; Zullo, 1966), but here too, as in the Caribbean, much further field work has been generated by the proposal to construct a sea-level canal across the Isthmus (Jones, 1972).

For the systematics included in this report we have drawn on the published material cited, and on the recent revision of the Balanus amphitrite complex (Henry and McLaughlin, 1975); but we have also made extensive use of new material, including the baseline survey collections made under the auspices of the Smithsonian Institution. The new material has posed many systematic problems, the solution of which will depend on further detailed studies of the eastern tropical Pacific species; the present account must therefore be regarded as provisional. However, it can be concluded that, in spite of the present differences in the respective ecosystems and the continuous separation since the late Pliocene or early Pleistocene, there is still considerable affinity at the species level between the barnacle faunas of the Caribbean and the eastern tropical Pacific. The cutting-off of the Caribbean from the Pacific and from that reservoir of greatest tropical diversity, the Indo-West Pacific, together with the general long-term deterioration in climate, must have contributed to the poorer present-day Caribbean barnacle fauna. The differences in ecosystems on the two sides of Central America, as discussed here, provide ample reasons for the notable differences that exist.

We would like to thank Dr. M.L. Jones for the loan of material from the National Museum of Natural History-Smithsonian Tropical Research Institute Panama Survey; Dr. Eve Southward for assistance in the field and with the literature; Dr. J.H. Wickstead for interest and advice; and Dr. Angeles Alvariño for the Spanish version of the abstract.

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STRUCTURE AND ECOLOGY OF CARIBBEAN CORAL REEFS

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Abstract

Until recently, Caribbean coral reefs have been interpreted as variants on general models described from reefs in the Bahamas and Jamaica; recent work in Panama, the Lesser Antilles and Belize has led to substantial revision of previous ideas. The status of Caribbean coral reefs thus needs fresh evaluation in comparison with better known Indo-Pacific reefs.

Work on reef morphology has concentrated on four areas: (1) It has been shown that, on some reefs, crustose coralline algae form structures comparable to those on Pacific reefs, their absence in the Caribbean having been hitherto one of the chief points of contrast between the two provinces; (2) Contrary to earlier generalizations, some Caribbean coral reefs do form intertidal reef flats; (3) Significant bioconstruction by sclerosponges, sediment production by Halimeda, and submarine lithification have been found on deep reef slopes (using submersibles) below the depth limits of scleractinian corals; (4) Evidence from bathymetry, shallow boring, seismic profiling and radiometric dating indicates that many Caribbean reefs rest unconformably on an erosion surface developed on older limestones, and broadly equivalent to the Thurber Discontinuity of the Pacific.

Sea-level curves, now available from Bermuda, Florida and Panama, define the time span over which present surface reefs have grown. There is also much evidence of the erosional, constructional and ecological effects of catastrophic storms on reefs. These data indicate that reefs are in a transitional state between unconstrained vertical upgrowth to the sea surface and lateral out-building with reef-flat formation. Stratigraphy of modern reefs and also of upraised Pleistocene reefs in Barbados suggests a successional sequence of reef development in response to sea-level change. Thus a deep reef community of massive corals (Montastrea, Diploria) may be replaced by a shallow, rough-water, ramose community (Acropora) and then a reef-flat community (Porites); this, in turn, may be replaced by a nonscleractinian community: first a Thalassia community, then Rhizophora and, finally, Avicennia and other mangroves. In interpreting such successions, it has been shown by recent work that modern reef communities may differ markedly from those in the immediately preceding geological record, and thus do not necessarily form a reliable guide to the nature of the reef frame. It is also suggested that catastrophic storm activity might play an important part in interrupting successional sequences in many parts of the Caribbean and in determining present patterns of coral growth.

Caribbean reefs are thus in a state of rapid ecological and morphological change consequent on recent sea-level history. This, rather than the gross discrepancies in reef-building potential previously hypothesized, may account for some of the differences classically described between the Caribbean and other major reef provinces. In spite of important advances in the knowledge of Caribbean reefs in recent years, however, it is important to recognize the reality of such differences in terms of diversity, morphology, structure and history.

Resumen

Hasta hace poco tiempo, los arrecifes de coral del Caribe habían sido interpretados como variaciones de modelos descritos en general sobre arrecifes de las Bahamas y Jamaica; pero trabajos recientes en Panamá, las Antillas Menores y Belice, han llevado a una revisión substancial de las ideas anteriores. Por lo tanto, la condición del arrecife de coral del Caribe requiere una nueva evaluación, en comparación con los arrecifes mejor conocidos del Indo-Pacífico.

Los trabajos sobre la morfología de los arrecifes se han concentrado en cuatro sectors: (1) Se ha demostrado que en algunos arrecifes el alga coralina costrosa forma estructuras comparables a las de los arrecifes del Pacífico, cuya ausencia en los del Caribe había sido hasta ahora uno de los puntos principales de contraste entre los dos; (2) En contra de ideas previas, algunos arrecifes coralíferos del Caribe si forman planos o terrazas intermarea; (3) Mediante el uso de sumergibles se han encontrado: bio-construcción considerable por esclero-esponjas, producción de sedimentos por *Halimeda*, así como también petrificación submarina, en declives profundos más allá de los límites de profundidad de los corales escleractinios; (4) Evidencia batimétrica, perforaciones a poca profundidad, perfiles sísmicos y datationes radimétricas indican que muchos arrecifes del Caribe descansan sin conformarse ella sobre una superficie de erosión equivalente a la Descontinuidad de Thurber en el Pacífico.

Los gráficos de niveles marinos de que ahora disponemos sobre las Bermudas, la Florida y Panamá, definen el lapso de tiempo transcurrido durante el crecimiento de los presentes arrecifes de superficie. También existe abundante evidencia de los efectos de tormentas catastróficas en la erosión, construcción y ecología del arrecife. Esos datos indican que los arrecifes están en un estado de transición entre el crecimiento vertical sin restricción hacía la superficie, y la expansión lateral conformación de arrecife plano. La estratigrafía de los arrecifes modernos así como también la de arrecifes Pleistocénicos resurgidos en Barbados, sugiere una secuencia de desarrollo del arrecife en sucesión, la cual responde a cambios de nivel del mar. De ahí que una comunidad de arrecife profundo constituida por coral masivo (*Montastrea*, *Diploria*) pueda ser reemplazada por una comunidad ramosa (*Acropora*) de poca profundidad y aguas agitadas, seguida de una comunidad de arrecife plano (*Porites*); y esto a su vez puede ser reemplazado por comunidades noescleractinias - primero, una comunidad de *Thalassia*, seguida por otra de *Rhizophora*, y finalmente *Avicennia* y otros mangles. Trabajos recientes sobre la interpretación de estas sucesiones han demostrado que comunidades modernas de arrecifes pueden diferir notablemente de aquellas que las han precedido inmediatamente en orden geológico, aunque esto no constituye necesariamente una guía fidedigna sobre la naturaleza formativa del arrecife. También se sugiere que tormentas catastróficas podrían jugar un importante papel en la interrupción de la secuencia de sucesiones en muchas partes del Caribe, y en determinar los patrones actuales de crecimiento del coral.

Los arrecifes del Caribe se encuentran, por lo tanto, en un estado de rápido cambio ecológico y morfológico consecuente con la historia de los cambios recientes del nivel del mar. Más que constituir discrepancias importantes en el potencial constructivo de los arrecifes, esa puede ser la causa de algunas de las diferencias clásicamente descritas entre el Caribe y otras regiones de arrecifes mayores. A pesar de los importantes adelantos realizados en el conocimiento de los arrecifes del Caribe durante los últimos años, es importante reconocer, sin embargo, la realidad de las diferencias existentes en términos de diversidad, morfología, estructura e historia.

1. INTRODUCTION

Research on Caribbean coral reefs has been the subject of three main groups of reviews, each with a different perspective and each based on specific types of field evidence and with an emphasis on particular areas. The first included those of Vaughan (1918, 1919) drawing on field studies of modern reefs in Florida, the Dry Tortugas, Cuba, Puerto Rico and Panama, and on an unrivalled knowledge of the geological development of the Atlantic reef fauna. Vaughan's findings led him to dispute many of the widely accepted ideas about the generality of the Darwinian model of reef development through subsidence. The next group of reviews came from geological studies initiated in the Bahamas by Newell and his associates (Newell et al.,1951; Newell and Rigby, 1957; Newell et al.,1959; Squires, 1958; Storr, 1964). Newell's conclusions drew on the contrasts between the Bahaman reefs and others he studied in Polynesia and, to a large extent, supported the earlier ideas of Vaughan and Agassiz that reefs in the western Atlantic were but inferior analogues of those in the Indo-Pacific. In summary, Newell (1959, 286) found that: "Extreme youth and temperatures still well below the optimum may explain characteristic low growth rates and immaturity of the West Indian reefs. Living West Indian reefs form only a thin veneer over submerged terraces of non-reef rocks".

Then in the late 1950s, T.F. Goreau began work in Jamaica, subsequently concentrating on Discovery Bay and drew detailed attention for the first time to the nature of reefs within the Caribbean basin. His extensive efforts with many students and collaborators were supplemented by studies elsewhere in the Caribbean: at Alacran in the Gulf of Mexico (Kornicker and Boyd, 1962; Hoskin, 1963), on the British Honduras barrier reef and atolls (Stoddart, 1962, 1963), on the Nicaraguan shelf atolls (Milliman, 1969), in Cuba (Kühlmann, 1970, 1970a, 1971, 1971a, 1974) and the Lesser Antilles (Adams, 1968; Lewis, 1960; 1975; Roos, 1964; Roberts, 1972). More recently, studies in Panama and the Virgin Islands have yielded data comparable in quality to those for Jamaica (Porter, 1972, 1972a, 1974; Adey, 1975). Much new information on the Caribbean coral fauna has been provided, notably from Curaçao, Aruba and Bonaire (Lang, 1970; Roos, 1971; Scatterday, 1974; Bak, 1975), Colombia (Pfaff, 1969; Geyer, 1969; Antonius, 1971; Erhardt, 1974; Geister, 1975), Grand Cayman (Raymont et al., 1976; Roberts, 1974; Rigby and Roberts, 1975), Jamaica (Wells and Lang, 1973; Wells, 1973) and Venezuela (Antonius, 1972; Olivares and Leonard, 1971; Rodriguez, 1959). Though Bermuda, Brazil and West Africa, as outposts of the Caribbean province, lie outside the scope of this review, it is worth noting that they too have been studied in greater detail than hitherto (Laborel, 1966, 1967, 1969, 1971, 1974). More data are available for Gulf of Mexico reefs near the limits of coral growth (Chavez et al., 1970; Emery, 1963; Kühlmann, 1975; Rigby and McIntire, 1966; Morelock and Koenig, 1967; Freeland, 1971; Edwards, 1971). Useful comparative surveys of a number of Caribbean and other reefs have been provided by Dahl et al. (1974). Finally, a major work by Frost and Langenheim (1974) has renewed interest in the history of the Caribbean coral fauna generally reviewed by Frost (1972) and greatly stimulated by Geister's (1976) remarkable discovery of the Pacific genus Pocillopora in Pleistocene reefs on San Andrés.

In consequence of this great extension in the range of data available for synthesis, the third, and most recent, series of reviews of Caribbean coral reefs (Glynn 1973b, Milliman 1973) have rejected or reconsidered many conclusions reached from earlier work in Florida and the Bahamas. Partly, this results from a simple substitution of type-areas: Newell's Bahaman model superseded Vaughan's Virgin Islands and Greater Antilles model and, in turn, made way for Goreau's Jamaican model with regional variations. But it has also been suggested that some features distinguishing the Caribbean from the other major reef provinces have been based on a partial, or even erroneous, apprehension of the facts, and the view is now widely held (e.g. Frost and Weiss 1975) that reefs in the Caribbean are, at least, the equal in geological potential and biotic diversity of those in the Indo-Pacific.

It might be asked whether, in view of these recent syntheses, a further review of Caribbean reefs is required. I believe it is, if only because some of the elements in the new Caribbean synthesis require examination, not only in a Caribbean context, but also in the wider perspective of reef development elsewhere in the tropics; it is also perhaps useful to note that Kühlmann's recent reviews of reef development in Cuba have yielded conclusions closer to those of Vaughan than to some other recent studies elsewhere in the Caribbean (Kühlmann, 1971b).

In this paper, therefore, rather than giving a meticulous review of what is known of Caribbean reefs - already so ably done by Glynn (1973b) and Milliman (1973) - I shall review elements of form, process and history with the specific aim of evaluating some recent generalizations. Any discussion of Caribbean reefs must necessarily begin with Goreau's general model of Jamaican reefs, and Table I reproduces the main features of reef zonation on the north coast at Discovery Bay (Goreau and Land, 1974). This scheme is based primarily on topographic features and scleractinian coral distributions, but the divisions also have broad relevance to at least two other conspicuous animal components of Caribbean reefs, the sponges and the octocorals (de Laubenfels, 1950; Beyer, 1961; Goldberg, 1973; Kinzie, 1973; Opresko, 1973).

TABLE I

Zonation of reefs at Discovery Bay, Jamaica

Back reef	Shore Lagoon
Reef crest	0.5-6 m including buttress zone, 1-10 m
Seaward slope or fore-reef	Fore-reef terrace to 10-15 m Fore-reef escarpment from 15 to 25-35 m
Fore-reef slope	Extending from 25-35 to 55-65 m, 150 m wide, angle 30-60°. Covered with platey Montastrea and with reef pinnacles up to 10 m tall; may be topped by a Montastrea sill reef
Drop-off	At 55-65 m
Deep fore-reef	From 55-65 m to more than 90 m, with a slope of 60-90°. Below 75 m a framework of sclerosponges rather than corals; the corals are mainly foliaceous forms of Agaricia, Mycetophyllia and sheet-like Montastrea

Source: Goreau and Land, 1974

2. FORM

Two main elements of form require discussion: the algal rim and reef flat, and the deeper reef slopes.

2.1 Algal Rim and Reef Flat

It has long been held (e.g., Stoddart, 1969) that pronounced algal ridges on the seaward edges of windward reefs are absent from the Caribbean, in contrast to reefs in, for example, the Marshalls, Tuamotus, Maldives and other areas of the Indo-Pacific. Perhaps partly in consequence, it has also been held that Caribbean reef flats are generally lower than those of the Indo-Pacific, and less frequently form drying intertidal surfaces (Caribbean tidal ranges are of course mainly microtidal, as opposed to the meso- and macrotidal ranges common in the Indo-Pacific). Milliman (1973, 42) has suggested that this difference in constructional algal activity is "the major ecological difference between Caribbean and Indo-Pacific coral reefs"; he suggests that the niche left vacant by the absence of crustose coralline algae is largely occupied in the Caribbean by the hydrozoan Millepora. At the same, it is true that several workers have earlier recognized weak analogues of Pacific algal rims on Caribbean reefs (e.g., the "Lithothamnion-Millepora ridge" of Newell et al. (1951, 22) at Andros, Bahamas, and the "Goniolithon pavement" of Stoddart (1963a, 77) at Glover's and Lighthouse Reefs, Belize), but such comparisons usually emphasized the differences between these forms and typical Indo-Pacific rims.

This apparent contrast between the reef realms has recently been challenged, first by Glynn (1973b, 285), following fieldwork in Panama, and then by Adey and co-workers in extensive studies in the eastern Caribbean (Adey, 1975; Adey and Burke, 1976). Now, it is even held that algal ridges - "it is clear" - are "nearly as pervasive in the Caribbean as they have been thought characteristic of the Indo-Pacific region" (Frost and Weiss, 1975, 23).

Such a conclusion must astonish those familiar with the extensive algal pavements and ridges which edge reef flats, themselves over a kilometre wide, and which dry completely at low spring tides, of a kind repeatedly described from the Indian and Pacific Oceans. Have such features simply been overlooked in the Caribbean? Are different features being erroneously equated? Is the comparison - and the conclusion - justified?

At the Holandés Cays, Glynn (1973b; also Porter 1972, 91) describes a terraced ridge 15 m wide, extending in spurs to a maximum width of 30-40 m, and standing at the edge up to 1 m above mean high water. Glynn compares this Panama ridge to the "boilers" of Bermuda and Puerto Rico. Rather similar features are described from St. Croix, Virgin Islands. Here, the highest levels range from mean sea-level to 0.2 m above MHWS (Adey, 1975; Adey and Burke, 1976 quote rather higher levels). Adey (1975, 2) comments: "They are truly algal ridges in that they are built above mean low water and not only is their upper carbonate framework dominantly crustose coralline, but their upper surfaces often support a rich fleshy algal flora of high biomass and productivity". From aerial reconnaissance and field study, Adey and Burke (1976) document the existence of these features from the Virgin Islands south, through the Lesser Antilles, to Grenada.

In discussing this evidence and comparing it with the Indo-Pacific, a distinction must be made between morphology and structure. First, morphology. In the Indo-Pacific, algal ridges where best developed are characterized by (a) a raised rim, several dm to a metre above the reef flat, and often tens of metres wide, rising from an algal pavement that may be some hundreds of metres wide; (b) location on the seaward edge of a reef flat which is commonly a high-standing abraded limestone surface, often more than 1 km wide, with corals growing only in hollows, channels, or toward the lagoonward edge; and (c) lateral continuity, at least on windward reefs and except where interrupted by major passes, and with only small-scale furrowing by surge channels. Thus defined, algal ridges may extend for tens of kilometres round individual reefs. The Caribbean features are quite clearly different, if only in scale, though Adey (1975, 30) has suggested that even the Tuamotu and Marshall Islands ridges originated as discrete "boilers" of the Caribbean type and have formed continuous ridges by coalescence.

There are two further features of particular note in the Caribbean: first, the discontinuity and patchiness of the so-called ridges exemplified, for example, by the highly irregular windward coast topography of an island such as Barbuda; and second, the general absence of anything comparable to an Indo-Pacific reef flat behind them. On the British Honduras reefs the reef flat or "reef pavement", usually more than 1 m deep, consists of a conglomeratic substrate of corals and other debris, well, but patchily, cemented for the upper 0.5-1 m but loose below, and with living corals growing over at least the seaward portion. Radiometric dates show that the superficial conglomerate is contemporary and the cement is of marine origin (James, Ginsburg, Marszalek and Choquette, 1976). By contrast, the reef flat or "reef plate" at Eniwetok and Bikini is a wedge of competent rock 1-4 m thick, several hundred metres wide, comprising corals in the position of growth 1 800-4 000 years old bevelled by subsequent erosion, and with its surface now standing at intertidal levels (Henny, Mercer and Zbur, 1974; Tracey and Ladd, 1974).

Second, structure: and here paradox abounds. It has long been recognized that prominent "algal ridges" in the Pacific are not necessarily constructional features. Thus, in Tahiti, Crossland (1939, 468) described the algal cover as "a mere skin over projections of reef rock", a situation similar to that at Rangiroa in the Tuamotus (Stoddart, 1969a). More recently, at the type site in the Marshalls, it has been shown that the prominent ridges comprise a rubble core about 4 400 years old covered with a veneer of coralline algae only 10-15 cm thick (Buddemeier *et al.*, 1975) (at other sites, of course, as shown by roofing of surge channels, active bioconstruction is certainly taking place). The point is that topographic evidence - whereby the ridge is recognized - does *not* imply construction by crustose coralline algae: the ridges, in their type localities and *often* where most prominent, may have more complex histories.

Adey (1975, 23) reports a rather similar situation in St. Croix where "the original outline of the *A. palmata* is obvious" beneath the algal skin. In Guadeloupe and Martinique, however, crustose corallines have been shown to form structures 3-5 m thick (Adey and Burke 1976). Where conditions allow, it is clear that algae are capable of significant construction in the Caribbean, and Adey (1975) quotes growth rates of crustose corallines comparable to those of the most rapidly growing corals. Nevertheless, the features so formed in the Caribbean are discontinuous, and Adey interprets them as intermediate early stages in growth from foundations at suitable depths following drowning by, and subsequent stillstand of, the Holocene sea.

It would appear, therefore, that the major difference between the Indo-Pacific and the Caribbean is not in the presence or absence of potentially ridge-building algae, but in the presence of suitable reef substrates at, or close to, present sea-level in the former area, but less commonly in the latter. The fact that most features described by Adey and Burke do not margin surface reefs, but occur as discrete patches, suggests that the major morphological difference lies in the inability of the Caribbean reefs to form wide, sea-level reef flats of the typical Indo-Pacific kind. It might further be recalled that the only Caribbean sites where significant algal construction has been claimed are on the Atlantic coasts of the Windward and Leeward Islands, subject to trade-wind surf, and in Panama, open to the longest fetch in the Caribbean basin; and it remains open to argument that one reason why ridges are not better developed in the Caribbean is that the reefs are not exposed to surf on the same scale as in the Indo-Pacific.

2.2 The Deep Reef Slope

Perhaps the most spectacular new information on Caribbean reefs comes from the zone hitherto almost entirely unknown, as a result of exploration of the deep fore-reef to depths of 300 m and more using submersibles. Such dives have been carried out in Jamaica (Lang 1974; Moore *et al.*, 1975; Colin, 1974), Belize (Lang, 1974; Lang *et al.*, 1975; Colin, 1974; Ginsburg and James, 1973, 1976), Bimini, Bahamas (Neumann and Ball, 1970), and Berry Islands, Bahamas (Porter 1973). The near-surface zonation of Goreau and Land (1974) in Jamaica (Table I) can now be extended to greater depths:

a) seaward slope. This comprises a terrace at 10-15 m, terminating in a fore-reef escarpment extending from 15 to 25-35 m;

b) fore-reef slope, from the foot of the escarpment, extending at an angle of 30-60° to depths of 55-65 m;

c) "drop-off", a pronounced inflection at 55-65 m, which marks a major boundary in substrate inclination and hence in illumination and sedimentation. The drop-off occurs at different depths in different areas: 30 m at Bimini, 18-64 m in the Berry Islands, 60 m on the Belize barrier reef and 60-70 m on Glover's Reef;

d) deep fore-reef, sloping at 60-90° and, in places, overhanging, extending from 55 to 114-145 m. At Bimini this cliff extends from 30-76 m, on the Belize barrier from 60 to 140 m and on Glover's Reef from 60 to over 300 m;

e) the island slope, a gentler inclination of 45°, extending to over 300 m at Discovery Bay consisting of bare rock, sediment streams and large talus boulders. At Bimini, the sediment slope extends from 76 to 222 m, below which there is a smooth rock surface with a uniform 5° slope, extending to 538 m. At such depths, the epifaunal cover is very low (less than 1 percent), but the infauna is yet to be studied.

Five remarkable discoveries have been made during these studies of the deeper slopes at Discovery Bay, though it has still to be demonstrated that they are of general occurrence.

First, it is now known that scleractinian corals extend to considerably greater depths than originally supposed. The limiting depth appears to be 90 m in the Bahamas, 98 m in Jamaica and 100 m in Belize, though, in general, they cease to be framework constructors at about 70 m, partly because of decreased calcification rates, partly because of relatively increased activity of bio-erosional organisms, partly because of the steepening inclination of the substrate. Aspect must be a significant control as well as inclination, and it is worth noting that the Discovery Bay reef is on a north-facing coast in about 18° N latitude.

Second, algae have been found to considerable depths in spite of very low illumination intensities (measurements have been made, in terms of surface light intensities, of 2-3 percent at 15 m depth in the Bahamas and 1 percent at 25 m depth in Jamaica). The calcareous green alga Halimeda is found to depths of 98 m in Jamaica and 100 m in Belize; crustose red algae are reported at 122 m in the Bahamas, 175 m in Jamaica, and a remarkable 250 m in Belize. Moor et al. (1976) have documented the geological significance of Halimeda as a deep sediment producer at Discovery Bay.

Third, Goreau and his co-workers first showed the importance of sclerosponges as bioconstructional agents on the deep fore-reef between 75 and 105 m, where they replace corals as the chief framework constructors. Several species are present, the most important being Ceratoporella nicholsoni and Stromatospongia vermicola (Hartman and Goreau, 1970; Lang et al., 1975). Sclerosponges are much less important at comparable depths on the Belize reefs, however, and it remains to be established how universally important they are in framework construction on the deep reef.

Fourth, boring sponges become increasingly important at the lower limits of coral growth, in weakening coral skeletons and holdfasts, and thus influencing the size and growth form of the corals which grow at these depths (Goreau and Hartman, 1963, 1966; Pang, 1973, 1973a; Rützler, 1974). Recent work by Rützler (1975) on the reefs of Bermuda and Belize yields rates of erosion by clionid sponges equivalent to the removal of a thickness of 0.1 mm/y, with extreme rates reaching 1 mm/y. Boring also yields substantial quantities of sediment: at Discovery Bay 5 percent of the island slope sediments are derived from the boring activities of clionid sponges (Moore et al., 1976).

Finally, the existence of rapid bonding of slope and reef-flat sediments by submarine lithification processes, involving cementation by Mg-calcite and also by aragonite, has been found to be a widespread process, yielding fabrics in some cases similar to those of intertidal beachrock, and probably of critical importance in maintaining the deep slopes of the deeper reef zones (Land and Goreau, 1970; Ginsburg and James, 1976; James et al., 1976).

3. SHALLOW BANKS AND REEFLESS AREAS

A corollary of Vaughan's view that Caribbean reefs are young and in process of development is that not all potential reef-growth sites are occupied by sea-level reefs. Within the Caribbean basin there are both isolated banks (Table II) and coastal shelves almost devoid of reefs. Most of the banks have maximum depths of 30-40 m. Horsfield (1975) has suggested regional tilting of the banks, with least depths near eastern Cuba and Haiti; the effects of this tilting, he believes, can also be demonstrated on individual banks. Thus, the surface of the Pedro Bank varies from 15 to 35 m depth in 130 km, and of the Morant Bank from 30 to 50 m over 120 km. Pedro Bank, with an area of 7 900 km^2, has been studied in detail by Dolan (1972). Dolan interprets the surface relief in terms of bevelling rather than tilting, and finds benches at 3-4 and 15-19 m, extensive flat areas at 31-40 m and a platform at 45-65 m.

TABLE II

Some submerged banks in the Caribbean Sea

Admiralty chart	Bank	Estimated mean depth (m)
450	Blossom	42.0
450	New	30.5
450	Walton	37.0
486	Bajo Nuevo	22.3
486	Pedro	23.2
486	Alice	25.0
762	Serranilla	23.0
762	Rosalind	27.8
762	Thunder	32.5
762	Un-named	33.0
762	Misteriosa	20.7
762	Quita Sueño	25.0
486	Morant	20.5

The last three of these he dates, by reference to the postulated stillstands on the Fairbridge Holocene eustatic curve, at 8 900-10 800, 10 800-12 000 and 12 500-17 000 y B.P., though this does not take into account the rates at which such extensive bevelling would have taken place. On Saba Bank, which has also been studied in detail, and which has an area of 2 000 km^2 and depths varying from 20 to 40 m, Van der Land (1976) describes several reefs rising to between -12.5 and -43 m (the shallower ones rising from shallower foundations and being in general wider and longer). The levels seem very variable and some of the reefs appear to be tilted.

Nevertheless, whether tilted or bevelled, the widespread near-accordance at shallow depths both of the isolated banks and the Nicaraguan, Honduran and Yucatan shelves, requires some explanation, as does the general absence or paucity of reefs rising from them.

Terraces are also commonly found on modern reef slopes and may have historical significance. On Barbuda there are levels at 20 and 55 m(Wigley, 1972), in the Dry Tortugas at 17-21 m (Jindrich, 1972), in Jamaica at 10-15 and 25-65 m (Goreau and Land, 1974), in the Bahamas at 6, 8, 20 and 35 m (Zankl and Schroeder, 1972), in the Cayman Islands at 7-10, ca 20, and 60-73 m (Roberts, 1974; Roberts et al., 1975; L. Hull and G. Potts, pers. comm.), and at San Andrés at 4 and 20 m (Geister, 1975; Kocurko, 1972). In the Dry Tortugas the 17-21 m shelf has been correlated with a stratigraphic discontinuity at 10 and 18.5 m beneath Garden and Loggerhead Keys. Stanley (1970) also regards the "10 fathom terrace" (circa 20 m) on the seaward reefs of Bermuda as an erosional feature.

It seems quite probable that the extensive bank surfaces at 20-30 m were exposed and subject to karst erosion during the last low stand of the sea, and were last submerged 9 000-10 000 years ago. Because of the rate of sea-level rise and the limited time available, it is unlikely that the form of the surfaces has been greatly altered by marine erosion since their submergence. However, marine erosion may be responsible for features such as caves, notches and terraces occasionally recorded at greater depths. Thus a wave-cut terrace has been noted at the Berry Islands, Bahamas at 64 m (Porter, 1973), a discontinuous notch at Bimini at 70 m (Neumann and Ball, 1970), and a shelf at 120-140 m and caves at 150-180 m on

Glover's Reef (Colin 1974). On the Yucatan Shelf, Logan et al. (1969) found evidence for stillstands at 29-37 m (tentatively dated at 8 000-9 000 y B.P.), 51-64 m (11 000 y), and 91-137 m (13 000-18 000 y).

If the bank surfaces are primarily karst-eroded features, strict accordance of level would not be expected. Uneven surfaces would thus be flooded by the transgressing sea at different times and at different rates. Reefs initiated at low levels, while the sea was rising rapidly, might be drowned before the transgression rate fell; conversely, by the time the rate of sea-level had slowed, many suitable substrates might be too deep for effective reef growth to take place.

These arguments have been developed on two levels: first, by a combination of topographic survey, seismic reflection profiling and drilling, Purdy (1974, 1974a) has shown conclusively that the reefs of the Belize barrier system mimic a pre-Recent karst topography developed on older reefs. Depths of the unconformity beneath the modern reef material in a series of cores were:

	(m)
Spanish Cay	19.5
Cocoa Plum Cay	9.2
Tobacco Cay	14.0-16.4
Spruce Cay	18.0
Laughing Bird Cay	18.3
Colson Cay	19.2
East Snake Cay	25.9

These depths are similar to those for the Dry Tortugas previously quoted and, probably, give a reasonable indication of the magnitude of reef construction under favourable conditions on suitable substrates in post-glacial time.

Second, in the eastern Caribbean, Macintyre has identified numerous submerged banks which he interprets as reefs initiated early in the transgression, but subsequently drowned (Macintyre, 1972; d'Anglejan and Mountjoy, 1973). These reefs cluster at 40 and 75-90 m depth. He suggests that the deeper ones may date from a stillstand at 15 000-16 500 y B.P. Whatever the age, these structures are evidence of abortive reef development of a kind apparently less common in Indo-Pacific. Among factors which could be responsible are: (a) decreased reef-building potential in the Caribbean, perhaps because of lower temperatures; or (b) the presence of substrates at levels too deep for reef growth to be continuous once initiated. Adey and Burke (1976) conclude that "existing Pleistocene shelf depth has been critical in determining the extent of reef development": thus shelves at depths of 15-18 m may carry modern reefs, but shelves deeper than 20-25 m in general do not.

4. RAISED REEFS AND SEA-LEVEL HISTORY

Extensive raised reefs occur throughout the West Indies and the Caribbean basin. In Florida, dates for both the Miami Oolite and the reefal Key Largo Limestone cluster round 130 000 y and suggest a last-interglacial sea-level at +10 m (Osmond et al., 1965). Similar dates by Broecker and Thurber (1965) suggest a sea-level close to the present level at 85 000, 130 000 and 190 000 y B.P. A further series of dates from the northern Bahamas range from 105 000 to 146 000, and cluster round 125 000-130 000 y (Neumann and More, 1975), suggesting a sea-level at +5.6 m at about 125 000 y B.P. Similar reefs fringing the north coast of Jamaica yield ages of 117 000-142 000 y (Moore and Somayajulu, 1974), and reefs of probably the same age fringe much of Cuba, Haiti, the Dominican Republic, the Cayman Islands (Ironshore Formation), and San Andrés (San Luis Formation). The evidence from the raised reefs of Barbados indicates periods of reef formation during relatively high sea-levels at 65, 82, 105, 125, 200, 350 and 500 thousand years B.P. (of the younger stands, only that at 125 000 y was higher than present sea-level; the others reached levels of -10 to -20 m) (Mesolella et al., 1973; Bender et al., 1973).

Undoubtedly the morphology of reefless banks and reef foundations has been influenced by these repeated Pleistocene high sea-level stands. By contrast, the present stand of the sea has been extremely brief. Leaving aside the data from the Mississippi Delta area, Holocene sea-level curves can be constructed for Panama, Bermuda and Florida (Bartlett and Barghoorn 1973, Macintyre and Glynn 1976, Neumann 1971, Scholl et al. 1969). These curves are similar in form though differing in detail; they indicate a rapid rise of sea-level to about -20 m at 8 000-9 000 y B.P., then a substantial reduction in the rate of rise, with the sea not rising above its present level since that time. According to these curves (Fig. 1), sea-level reached within 5 m of its present level between 2 500 and 6 000 y B.P., and has continued to rise slowly.

5. DIVERSITY AND GROWTH POTENTIAL OF CARIBBEAN REEFS

Newell's view of the "low growth rates and immaturity" of West Indian reefs has already been mentioned. It derives partly from the low diversity of scleractinian corals in the Caribbean area, and partly from the growth rates measured by Vaughan (1915) for common Caribbean corals. The contrast in diversity between the Caribbean and the Indo-West-Pacific is apparent at the generic level (30-35 genera on most Caribbean reefs compared with 55-65 in the Indo-West-Pacific) and at the species level, notably in the representation of particular genera of major hermatypes (e.g., three species of Acropora in the Caribbean compared with over 200 in the Indo-Pacific, and three of Porites compared with 50). Many abundant and prolific Indo-Pacific genera (such as Pocillopora and Montipora) are now absent from the Caribbean.

The best-known coral fauna in the Caribbean is that of Jamaica, which Goreau's work increased from the 41 species known in 1959 to 64 in 1973 (40 being hermatypic), and also Panama, with 65 species (including 49 hermatypes) (Wells and Lang, 1973, with new taxa in Wells, 1973; Porter, 1972). It seems probable, as Glynn (1973b, 274-275) suggests, that comparable diversities will be found elsewhere as the intensity of study increases. But even if "these data indicate that the coral fauna in the entire Caribbean area may be richer than formerly suspected" (Glynn, 1973b, 275), the disparity between it and the Indo-West-Pacific remains substantial. At the species level, Marshall Islands reefs have four times as many scleractinian corals as Jamaica and, at the other end of the Indo-Pacific realm, the reefs of Madagascar have twice as many species. In very general terms, for every coral species on a Caribbean reef the Indo-Pacific reef has a genus, often represented by many species. Perhaps the contrast is most apparent when viewing the great diversity, both of species and of forms, in the single genus Acropora on reefs of, for example, the Great Barrier system, and comparing them with the representation of the genus on the reefs of Belize, the Cayman Islands or Barbuda. Parenthetically it may be added that the diversity difference between the realms extends to most other reef-dwelling groups, except perhaps for the Mollusca, though there is some danger in making inter-realm rather than inter-reef comparisons. Thus, there are 150 species of West Indian echinoderms compared with over 1 000 Indo-Pacific species (Clark, 1976); the 400 species of reef fish in Florida and 500 in the Bahamas compare with 1 500 on the Great Barrier Reef and over 3 000 in the Indo-West-Pacific (Goldman and Talbot, 1976); the 400 species of decapod crustaceans in the Caribbean compare with 1 200 species in the Australian region (Yaldwyn, 1973). Unfortunately we do not have comparable information on diversities on individual reefs of similar sizes in the two realms.

The early inference of differential growth rates between corals in the Indo-Pacific and the Caribbean is difficult to sustain since, as Glynn (1973b) pointed out, growth rates were compared between areas of very different environmental characteristics. Vaughan's early measurements from Florida and the Dry Tortugas, particularly, were from areas subject to low temperatures, especially in winter. More recent work by Lewis et al. (1968) in Barbados and Jamaica has revealed growth rates in major reef-building corals considerably higher than those determined by Vaughan, and comparable with rates recently measured in Hawaii and Samoa by Maragos (1972).

It also seems probable that, once established, Caribbean reefs have net growth rates, as established by C^{14} profiles, comparable with those of the Indo-Pacific. Rates of reef growth have been determined in Barbados of 1-3 m/1 000 y (Mesolella et al., 1970), from Belize

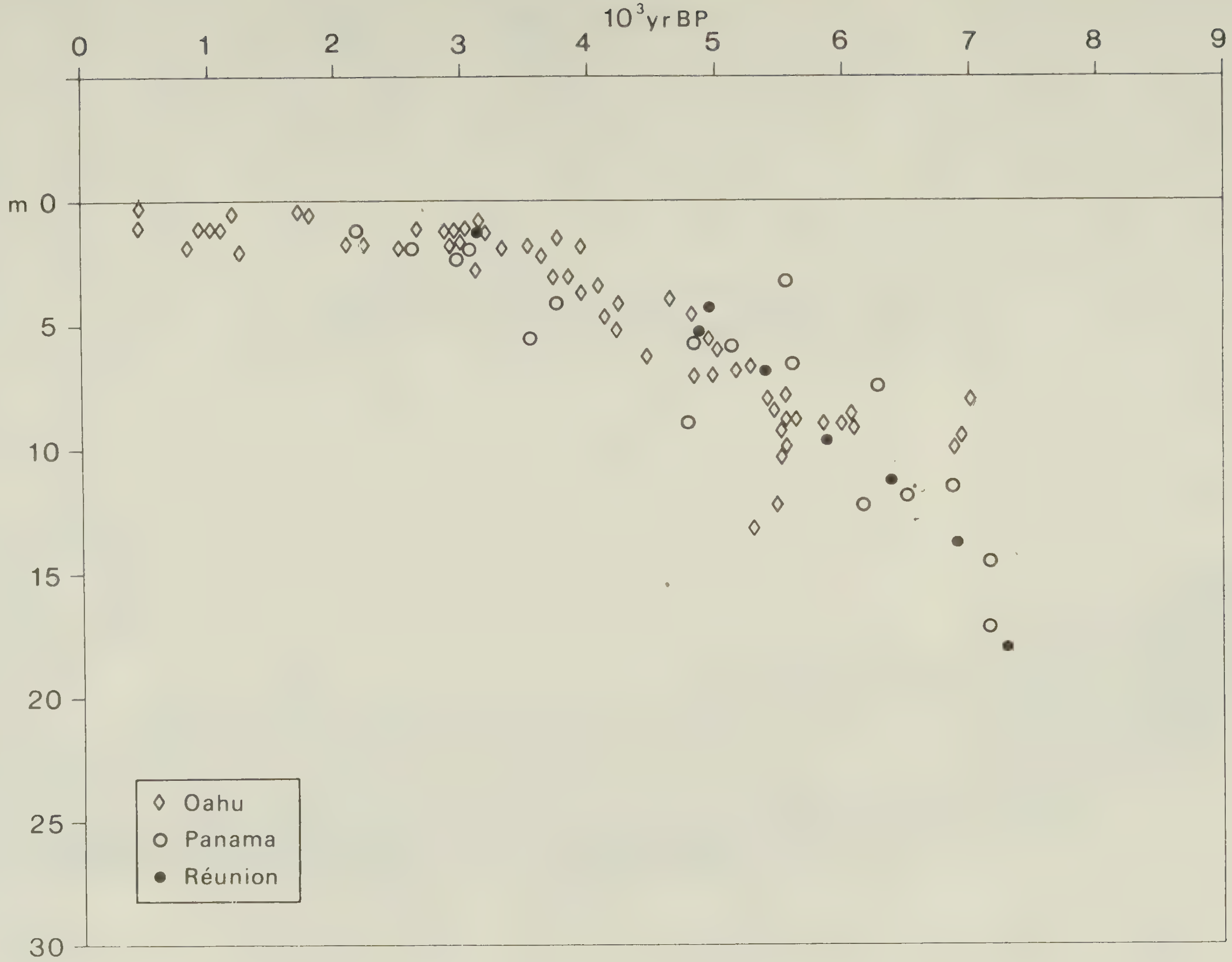

Fig. 1 Recent rise of sea-level indicated by radiometrically dated samples from borings in fringing coral reefs at Oahu, Panama and Réunion. Data from Easton and Olson (1976), Macintyre and Glynn (1976) and Montaggioni (1976)

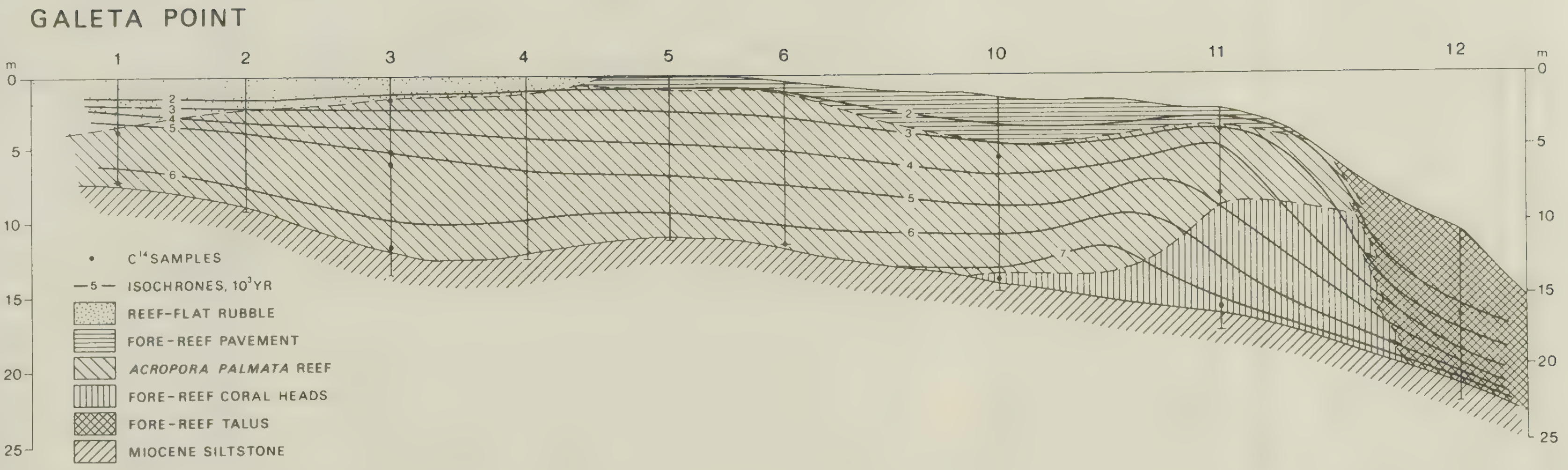
GALETA POINT
m
0
5
10
15
20
25
1
2
3
4
5
6
10
11
12
2
3
4
5
6
7
C^{14} SAMPLES
—5— ISOCHRONES, 10^{3}YR
REEF-FLAT RUBBLE
FORE-REEF PAVEMENT
ACROPORA PALMATA REEF
FORE-REEF CORAL HEADS
FORE-REEF TALUS
MIOCENE SILTSTONE

Fig. 2 Profile of the Galeta Point fringing reef, Panama, showing major communities and isochrones established by radiometric dating (from Macintyre and Glynn, 1976)

of 1.1–5.0 m/1 000 y (mean 2.7) (Purdy, 1974; 1974a), in Panama of 1.57–10.8 m/1 000 y (mean 3.9) (Macintyre and Glynn, 1976), for Florida of 4.3–8.5 m/1 000 y (Hoffmeister and Multer, 1964), for Jamaica of 0.2–1.0 m/1 000 y (Land, 1974), and for the Virgin Islands of up to 10.8 m/1 000 y (Adey, 1975). These figures compare with rates of 1.5–2 m/1 000 y at Mururoa in the Tuamotus and of 2.3–3.7 m/1 000 y at Eniwetok in the Marshall Islands (Lalou *et al.*, 1966; Thurber *et al.*, 1965). Most of these rates are for *Acropora* reef or equivalent rapid bioconstructors; massive corals and clastic sequences generally have net accretion rates of less than 1 m/1 000 y. Actual construction is, however, constrained by sea-level on the one hand and by substrate depth on the other, and as a result the actual thickness of Holocene reefs in the Caribbean area is probably not more than 10–20 m. Moreover, in spite of the apparent comparability in rates, it must be recalled that the magnitudes of reefs, measured by linear dimension as well as thickness, are substantially less in the Caribbean than in many Indo-Pacific areas. The problem of the Caribbean reefs thus becomes one not of explaining differences in the behaviour of the organisms but of explaining why broadly comparable organisms have not built broadly comparable edifices

6. SUCCESSIONAL SEQUENCES

It is clear from what has been said that Caribbean reefs, at present, are in a stage of transition from vertical growth during a period of rising and now stable sea-level, during the Holocene transgression, to lateral growth constrained by the present sea-air interface. Hence we might expect changes in the broad composition of the reef as the reef adjusted to these changing external constraints and also transformed its own environment by growth. Early successional suggestions of the replacement of a deeper water *Montastrea* community by a shallow *Acropora* community by Goreau (1959) in Jamaica were confirmed by Mesolella *et al.*, (1970) in their study of the raised reefs of Barbados. The model was extended by Macintyre and Glynn (1976) in drilling through a fringing reef at Galeta Point, Panama (Fig. 2), by Bonet (1967) at Alacran, and by Welch (1962), who attempted to link the reef sequence with other shallow tropical marine communities in Puerto Rico. In Panama, the thin recent reef (maximum thickness 12 m, age less than 7 000 y) comprised a basal community of massive corals, an *Acropora palmata* community, a reef-flat community of *Millepora*, *Agaricia*, *Porites* and *Diploria*, and a back-reef community of muddy sand and coral rubble up to 3 m thick. The transition between the *Acropora* and the reef flat communities occurred about 3 000–4 000 y B.P., when the rate of rise of sea-level markedly decreased, and *A. palmata* is no longer a significant component of the living reef.

In the eastern Caribbean, Adey and Burke (1976) found a rather comparable sequence developed over a similar time-span: a lower reef of *Diploria* and *Montastrea* with coral and mollusc rubble (comparable to Goreau's *Montastrea* zone) in depths of 6–20 m; a reef of *A. palmata* in 0.6–6 m; a community of crustose corallines with *Millepora* in shallow-water exposed situations; and, finally, a zone of fleshy-algal pavements dominated by *Sargassum*. In modern reefs of the northern Bahamas, Zankl and Schroeder (1972) found a transition between a shallow *A. palmata* community and a deeper *Montastrea*-*Diploria*-*Porites* community at about –3 m.

This evidence, from both modern reefs and the recent geological record, may be summarized and extended in the following tentative sequence of communities:

a) a deeper reef of *Montastrea* and *Diploria*

b) a shallow reef of *Acropora palmata*

c) a cap of crustose coralline algae, *Millepora* and *Agaricia* on exposed reef edges

d) a shallow reef flat community of *Diploria*, *Porites* and *Agaricia*

e) a back-reef facies of sand and rubble with sea-grass meadows, notably *Thalassia testudinum*, *Cymodocea manatorum* and *Diplanthera wrightii* (Scoffin, 1970)

f) mangrove communities with *Rhizophora* mangle as pioneer

Such a sequence could readily be extended into deeper water by including the zones already described from Discovery Bay and elsewhere, but it is likely that these bear a spatial rather than a temporal relationship to the sequence just outlined.

This scheme is highly simplified and, undoubtedly, will not fit many reef areas; it is also derived almost exclusively from sloping reef substrates, and Van der Land (1976) has noted the absence of zonation and of dominant species on the horizontal planar substrates of the shallow upper surface of the Saba Bank. It is a matter of common observation, moreover, that many corals have wide depth tolerances and appear in more than one zone. Montastrea, for example, is found in shallow, intermediate and deeper waters. To some extent, colonies can be distinguished in different depths by growth form and calyx detail (Lewis, 1960), but Scatterday (1974) has suggested at Bonaire that deep and shallow Montastrea zones are best distinguished by the presence or absence of less common agariciid, mussid and other indicator corals. It is also noteworthy that M. cavernosa replaces M. annularis in sub-optimal situations of temperature and turbidity on a number of reefs (Opresko, 1973, 485). In a similar way, Manicina areolata, often taken to be a characteristic coral of shallow reef flats and grass beds, is found at depths of 24-65 m in the Virgin Islands and St. Lucia, at 28-37 m at Bonaire and at 30-40 m on the Cayman Bank (though absent from the shallow reefs of Grand Cayman itself).

The primary control on the successional sequence is proximity to sea-level but, as Adey and Burke (1976) point out, this boundary will have changed considerably during the recent history of many Caribbean reefs. Thus, in the Virgin Islands, the Diploria-Montastrea reef commenced growing in water 5-10 m deep between 4 000 and 6 000 y ago; sea-level has since risen by 5-10 m, so that parts of this reef are now at anomalously low levels of 10-20 m.

A second control, however, is storm activity, particularly in fragmenting rapid-growing ramose corals and conferring a selective advantage on more massive, but slower-growing, forms. There have been many detailed studies of hurricane effects in Florida (Ball et al., 1967; Perkins and Enos, 1968), the Bahamas (Perkins and Enos, 1968) and Puerto Rico (Blynn et al., 1964), and these have been reviewed, together with studies of Indo-Pacific storms, by Stoddart (1971). It appears that minor storms may have only short-term effects on the reef, but continued surveys of the exceptional Hurricane Hattie of 1961 on the Belize reefs suggests that recovery will take many decades (Stoddart, 1963, 1965, 1969b, 1974). Jindrich (1972) has suggested that hurricanes are responsible for the prevalence of rubble-covered reef-flats and shoal areas on some Caribbean reefs, by preventing a successional sequence of ramose Acropora species from constructing a permanent growth framework. Hurricanes are confined to the northern part of the Caribbean, and one might thus expect significant differences in form, structure and community composition between reefs in Florida, the Bahamas, the Dry Tortugas and Belize, in contrast, for example, with reefs in Panama, Colombia and Curaçao. It is possible that some of the differences Glynn finds on the reefs of Panama, compared with generalizations about Caribbean reefs derived from other areas, results partly from this major environmental difference. Glynn himself (1968) has also drawn attention to a further contrast between the northern and southern Caribbean areas in thermal regime, in recording the effects of thermal stress on mass mortalities of reef-flat animals in shallow situations in Puerto Rico.

7. CONCLUSION

In this brief review I have attempted to evaluate some of the many new ideas and observations resulting from the great expansion of work on Caribbean reefs since the 1950s, by reference both to a wider spatial perspective in the Indo-Pacific and also by placing the modern development of Caribbean reefs into a geological perspective of the later Pleistocene. While many of the new discoveries apparently contradict long-established generalizations, there nevertheless remain real and substantial differences between the Caribbean and the Indo-Pacific, which may however reflect incidents in geological history rather than substantial differences in the nature of the reef-building organisms themselves. At the same time, it would be misleading to exaggerate the magnitude of Recent Caribbean reef construction, which cannot be compared with that of some great atoll chains of the Indo-Pacific or the Great Barrier Reef of Australia. The recent reviews of Caribbean reefs by Glynn and Milliman themselves define many of the contradictions between past studies and more recent work;

but in spite of the apparent differences between their views on many subjects, each comes to a conclusion similar to the position put forward in this paper, and which, on examination, proves not to be mutually contradictory and which also provides a key to the distinctiveness of the Caribbean reefs at the present time. For Milliman (1973, 44), "one of the most obvious differences between Caribbean and Indo-Pacific reefs is the lack of extensive reef development in the Caribbean"; while for Glynn (1973b, 291), "present-day Caribbean reef communities have the potential to develop similar structures as Indo-Pacific reefs under comparable meteorological and hydrographic conditions".

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BIOLOGICAL INVESTIGATIONS IN A TROPICAL LAGOON, GRAND CAYMAN, BRITISH WEST INDIES

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CONTENTS

1. INTRODUCTION
2. LOCALITY
3. METHODS
4. RESULTS
5. DISCUSSION
6. ACKNOWLEDGEMENTS
7. REFERENCES

Abstract

Recent studies of the North and Little Sounds, Grand Cayman, have revealed 98 species of marine flora and 520 species of marine fauna. Five distinct ecological regions were recognized, and observations indicated these to be controlled by the prevailing physical, topographical, and geological conditions. Some quantitative data are given, and a checklist is included for the principal species.

Resumen

Algunos estudios realizados recientemente en North and Little Sounds, Gran Caimán, han revelado la presencia de 98 especies de flora marina y 520 especies de fauna marina. Se han reconocido cinco regiones ecológicas distintas y las observaciones hechas han indicado que sus peculiaridades dependen de las condiciones físicas, topográficas y geológicas. Se presentan algunos datos cuantitativos y se incluye una lista de control para las principales especies.

1. INTRODUCTION

The marine biota of Grand Cayman has attracted the attention of several researchers. The flora has been described by Taylor (1969) and collections were made by W. Kings (1938) and, more recently, by G.R. Proctor. Abbot (1958) made a comprehensive collection of the marine molluscs and Rigby (1969) and Roberts (1973) have recorded several species of scleractinian corals. In 1938 the Oxford University Cayman Island Biological Expedition collected a variety of marine biota. The environments and organic communities of North Sound were studied by Roberts (1971).

The present paper discusses the results of a detailed survey of the flora, fauna and environments of the North and Little Sounds.

Five distinct biological communities are recognized, and the biota and environments of these areas are described.

2. LOCALITY

Grand Cayman is situated on latitude 19° 20' N and longtitude 81° 20' W, 120 mi WNW of Jamaica (Fig. 1).

The North and Little Sounds (Fig. 2) together form a large lagoon of some 85 km^2, bordered to the North by a fringing reef and surrounded on their other sides by a low profile, Recent and Pleistocene carbonate terrain. The land border supports an almost continuous strand of mangrove vegetation, varying in width from a few metres to several kilometres.

The tidal range in the area rarely exceeds 45 cm and, whereas tidal flushing periods are short near the reef crest, estimates for complete flushing of the interior of North Sound amount to 30 d (Darbyshire *et al.*, 1976).

Winds are predominantly easterly, creating a sheltered western seaboard and an exposed eastern coastline. Surface water temperatures range from 24.5°C in December to 30.0°C in July.

3. METHODS

The study was undertaken between May 1974 and July 1975 as part of the Marine Natural Resource Survey of the island (Raymont *et al.*, 1976). Data were collected from a total of 79 stations arranged on a grid pattern to cover the Sound; 37 of these stations were revisited to assess seasonal variation in the biota. At each station physical parameters such as water temperature, water depth, sediment depth and water clarity (determined by horizontal Secchi disc readings 1 m below the water surface) were measured. *In situ* macro-fauna and flora counts were made, using a 1/4 m^2 and a 10 m transect delineated by a 2 m pole. Epifauna were collected with a D-shaped handnet skimmed across the bottom by a diver swimming at full speed for a period of one minute. Infauna were sampled by removing samples of the benthos with a fork. Sediment samples were taken and two Naturalist dredge towns were completed over a distance of 150 m.

In addition to station sampling, a transect across the Sound was made using a Venturi-type suction pump to collect total inbiota and epi-biota from a 1/4 m^2 (Brook, 1974), the flora and fauna being collected in fine mesh bags.

4. RESULTS

A total of four species of marine angiosperms, 94 species of marine algae and 520 species of macro-fauna were collected; the identified species of each group are listed in Tables I and II.

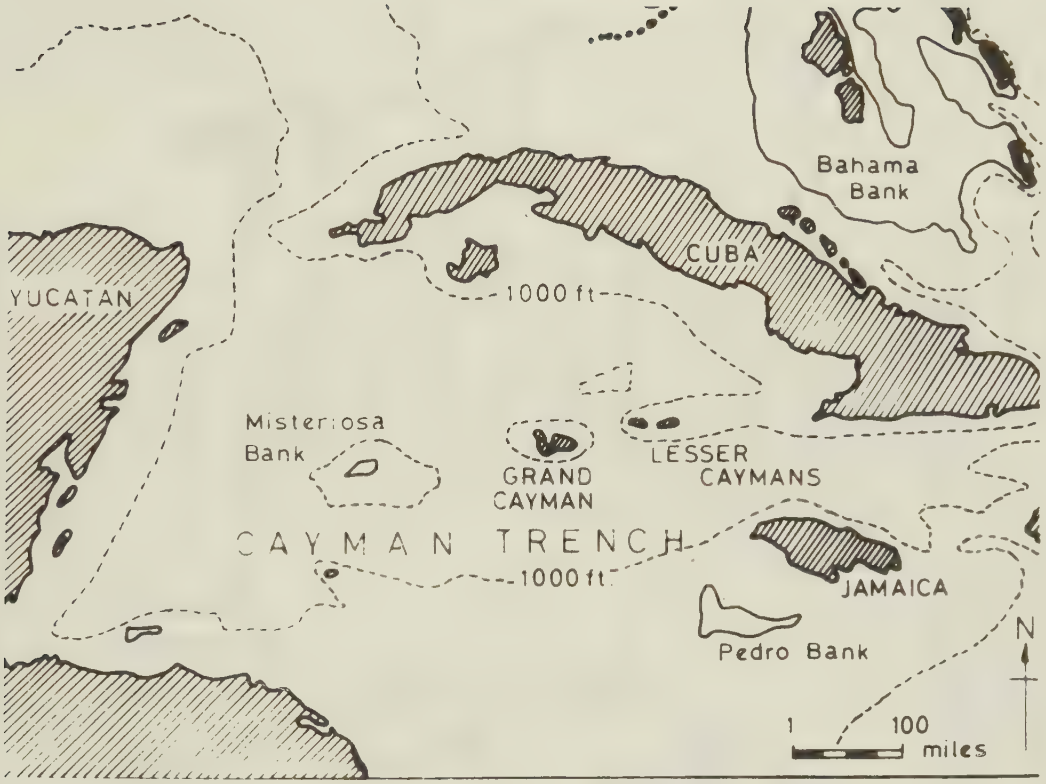
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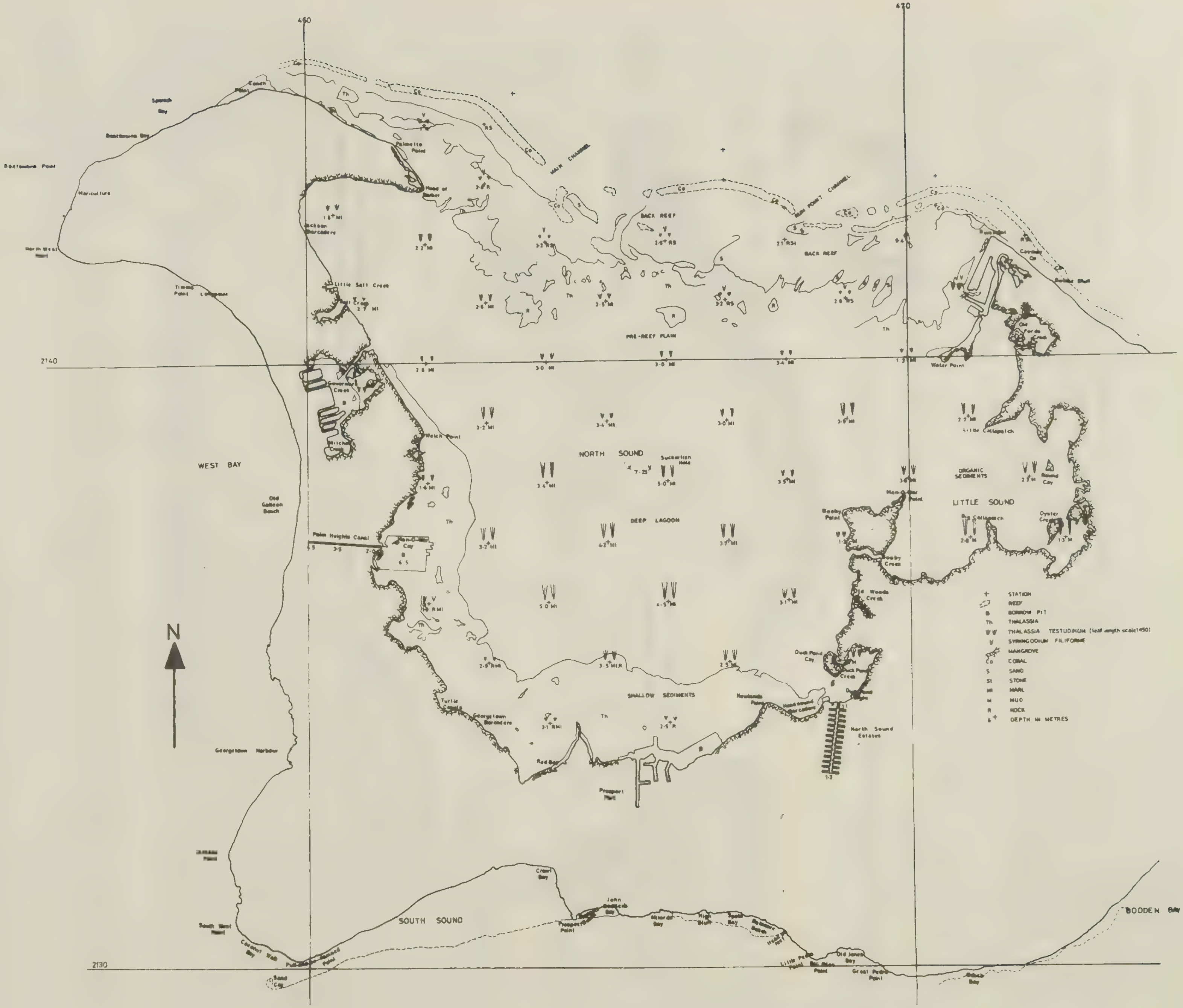
Fig. 1 Regional location of the Cayman Islands (by kind permission of the Cayman Island Government)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Georgetown Harbour
South West Point
Coconut Walk Bay
Sand Cay
SOUTH SOUND
Prospect Point
John Crookhead Bay
Crown Bay
BODDEN BAY
Boatswains Point
Boatswains Bay
Spanish Bay
Conch Point
Mariculture
North West Point
Timms Point
Palmetto Point
Head of Barker
Jackson Barcadere
Little Salt Creek
Governors Creek
Welch Point
Palm Heights Canal
Man-O-War Cay
Turtle Crawls
Georgetown Barcadere
Red Bay
Prospect Point
Newlands Point
North Sound Estates
Duck Pond Cay
Old Woods Creek
Booby Point
Booby Creek
Man-O-War Point
Water Point
Little Cattapatch
Big Cattapatch
Round Cay
Oyster Creek
Old Forde Creek
MAIN CHANNEL
RUM POINT CHANNEL
BACK REEF
PRE-REEF PLAIN
NORTH SOUND
Suckerfish Hole
DEEP LAGOON
SHALLOW SEDIMENTS
LITTLE SOUND
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B BORROW PIT
Th THALASSIA
THALASSIA TESTUDINUM (leaf length scale 1:50)
SYRINGODIUM FILIFORME
MANGROVE
Co CORAL
S SAND
St STONE
MI MARL
M MUD
R ROCK
6+ DEPTH IN METRES

Fig. 2 The North and Little Sound showing the communities and their major characteristics. Scale 1:75 000

TABLE I

The benthic flora of North and Little Sounds, Grand Cayman

	Shallow Sediment Community	Organic Sediment Community	Deep Lagoon Community	Pre-Reef Plain Community	Back-Reef Community
ANGIOSPERMS					
Thalassia testudinum	+	+	+	+	+
Average leaf count for 1 m^2	496	560	520	668	0
Average leaf length	13	40	42	16	0
Syringodium filiforme	+	0	0	+	+
Halodule beaudettei	+	0	0	0	0
Halophila englemanni	0	+	0	0	0
ALGAE					
CHLOROPHYTA					
Ulotrichales					
Enteromorpha	+	0	0	0	0
Cladophorales					
Chaetomorpha brachygona	0	+	0	0	0
C. geniculata	0	0	0	0	+
C. linum	0	+	0	0	0
C. nodosa	0	0	0	0	+
Chaetomorpha sp.	+	0	0	0	0
Cladophora howei	+	0	0	0	0
Cladophora sp.	+	0	0	+	0
Siphonocladiales					
Acetabularia crenulata	+	0	0	+	+
Anadyomene stellata	+	0	0	+	+
Batophora oerstedii	+	0	0	+	0
Cladophoropsis membranica	+	0	0	+	+
Dasycladus vermicularis	+	0	0	0	0
Dictyosphaeria cavernosa	+	0	0	+	+
Neomeris annulata	+	0	0	0	+
Valonia macrophysa	+	0	0	0	+
V. utricularis	+	0	0	+	+
V. ventricosa	+	0	0	+	+
Siphonales					
Avrainvillea longicaulis	+	0	0	0	0
A. nigricans	+	+	+	+	+
A. rawsonii	0	0	+	0	0
Bryopsis plumosa	+	0	0	0	0
Caulerpa ashmeadii	+	+	0	0	0
C. cupressoides	+	0	0	+	+
C. mexicana	+	+	0	0	0
C. paspaloides	+	+	0	+	0

Continued

TABLE I (Continued)

	Shallow Sediment Community	Organic Sediment Community	Deep Lagoon Community	Pre-Reef Plain Community	Back-Reef Community
Siphonales					
C. prolifera	+	+	0	0	0
C. racemosa	+	0	0	0	+
C. sertularioides	+	+	0	0	0
C. verticillata	+	0	0	0	0
Halimeda discoidea	0	0	0	0	+
H. incrassata	+	+	+	+	+
H. monile	+	+	+	+	+
H. opuntia	+	0	0	+	+
H. tuna	+	+	0	0	+
Penicillus capitatus	+	+	0	+	+
P. dumetosus	+	+	0	+	0
P. lamourouxii	+	+	+	+	0
Rhipocephalus phoenix	+	+	+	+	0
Udotea flabellum	+	0	0	+	+
U. occidentalis	+	0	0	+	0
PHAEOPHYTA					
Dictyotales					
Dictyota cervicornis	0	0	0	0	+
D. dentata	0	0	0	0	+
D. dichotoma	+	0	0	+	+
D. divaricata	+	0	0	+	+
D. linearis	+	0	0	+	0
D. volubilis	0	0	0	0	+
Dictyotales					
Dilophius alternans	0	0	0	0	+
Padina sp.	+	0	0	+	+
Stypodium zonale	0	0	0	0	+
Pocockiella variegata	0	0	0	+	+
Fucales					
Sargassum hystrix	0	0	0	0	+
S. platycarpum	0	0	0	0	+
S. polyceratium	0	0	0	+	+
Turbinaria tricostata	0	0	0	0	+
Punctariales					
Hydroclathrus clathratus	0	0	0	0	+
RHODOPHYTA					
Nemalionales					
Galaxaura sp.	0	0	0	0	+
Liagora sp.	0	0	0	0	+
Gelidiales					
Wurdemannia sp.	+	0	0	0	0
Cryptonemiales					
Amphiroa fragilissima	0	0	0	+	+
A. rigida	0	0	0	+	+
A. tribula	0	0	0	0	+
Dudressnya sp.	+	0	0	0	0
Fosliella sp.	+	0	0	+	+

Continued

TABLE I (Concluded)

	Shallow Sediment Community	Organic Sediment Community	Deep Lagoon Community	Pre-Reef Plain Community	Back-Reef Community
Cryptonomiales					
Gonioliothon sp.	0	0	0	0	+
Jania sp.	+	0	0	+	+
Lithothamnion sp.	0	0	0	0	+
Melobesia sp.	+	0	0	+	+
Peysonnelia sp.	0	0	0	0	+
Gigartinales					
Gracilaria cylindrica	+	0	0	+	+
G. debilis	0	0	0	0	+
Hypnea cervicornis	0	0	0	0	+
H. cornuta	+	0	0	0	0
H. musciformes	+	0	0	+	+
H. spinella	0	0	0	0	+
Rhodymeniales					
Champia parvula	+	0	0	0	+
Coelarthrum albertisii	0	+	+	0	0
Lomentaria rawitsheri	0	0	0	0	+
Ceramiales					
Acanthophora spicifera	+	0	0	+	+
Antithamnion sp.	+	0	0	+	+
Centroceros sp.	+	0	0	+	+
Ceramium sp.	0	0	0	+	+
Chondria dasyphyla	+	0	0	+	0
Chondria sp.	+	0	0	+	+
Ceramiales					
Crouania sp.	0	0	0	0	+
Dasyapedicellata	+	0	0	+	+
Digenia simplex	0	0	0	+	+
Heterosiphonia gibbesii	+	0	0	0	0
Hypoglossum tenuifolium	+	0	0	0	0
Laurencia intricata	+	0	0	0	0
L. obtusa	+	0	0	+	0
L. poitei	+	0	0	+	+
L. microcladia	0	+	0	0	0
L. papillosa	0	0	0	+	+
Polysiphonia	+	0	0	+	+
Spyridia filamentosa	+	0	0	+	+
Wrangelia sp.	+	0	0	+	0
Wrightiella blodgetti	+	0	0	0	0

+ = present

0 = absent

TABLE II

The major groups and principal species of invertebrates from North and Little Sound

	Shallow Sediment Community	Organic Sediment Community	Deep Lagoon Community	Pre-Reef Plain Community	Back-Reef Community
PORIFERA					
No. of species 18;					
Principal species,					
Chondrila nucula	+	0	0	+	0
Haliclona virdis	+	0	0	+	0
Tethya diploderma	+	0	+	+	0
Spheciospongia sp.	+	0	0	+	0
COELENTERATA					
No. of species 37;					
Principal species,					
Cassiopea xamachana	0	+	0	0	0
Goniopsis sp.	+	+	+	+	0
Bartholomea annulata	0	0	0	+	0
Condylactis sp.	+	0	+	+	0
Plexaura homale	+	0	0	+	+
Acropora cervicornis	0	0	0	0	+
Agaricia agaricites	0	0	0	0	+
Siderastrea siderea	0	0	0	0	+
S. radians	+	0	0	+	+
Porites astreoides	+	0	0	+	+
P. porites	0	0	0	0	+
COELENTERATA					
Porites divaricata	+	0	0	+	0
P. furcata	0	0	0	0	+
Pavia fragrum	+	0	0	0	+
Diploria clivosa	0	0	0	0	+
D. labyrinthiformis	0	0	0	0	+
D. strigosa	0	0	0	0	+
ANNELIDA					
No. of species 50;					
Principal species,					
Hermodice carunculata	+	0	0	+	+
Eunice rubra	+	0	+	+	+
Cistenides gouldii	0	+	+	+	0
Ammotypane aulogaster	+	+	0	+	0
Sabella melanostigma	0	+	0	0	0
Loimia sp.	+	+	+	+	+
Polyodontes lupina	+	0	0	+	0

Continued

TABLE II (Continued)

	Shallow sediment Community	Organic Sediment Community	Deep Lagoon Community	Pre-Reef Plain Community	Back-Reef Community
MOLLUSCA					
No. of species 120;					
Principal species,					
Gastropoda					
Bulla occidentalis	+	+	0	+	0
Cerithium eburneum	+	+	+	+	0
C. literatum	0	0	+	+	0
Fasciolaria tulipa	+	+	0	+	0
Prunum apicinum	0	+	0	+	0
Modulus modulus	+	+	+	+	0
Murex pomum	0	0	0	+	0
Smargardia viridis	0	0	0	+	0
Tegula fasciata	+	0	+	+	0
Astraea phoebia	+	+	+	+	0
Turbo castaneus	0	0	+	+	0
Chelidonura	+	0	0	+	0
Elysia sp.	0	0	+	+	0
Godium rubrolineata	+	+	+	+	0
Strombus gigas	0	0	+	+	+
Cassis tuberosa	0	0	0	+	+
Charonia variegata	0	0	0	0	+
Bivalvia					
Arca inbricata	+	0	0	+	0
Americardia media	+	+	+	+	0
Codakia costata	0	+	+	+	0
Aequipecten gibbus	+	+	+	+	0
Pinctada radiata	+	+	+	+	0
Chione cancellata	0	+	+	+	0
Pitar fulminata	+	+	+	+	0
Anodontia alba	0	+	+	0	0
Ctena orbiculata	+	+	+	+	0
Laevicardium laevigatum	+	+	+	+	0
Scaphopoda					
Dentalium antillarum	+	0	0	+	0
ARTHROPODA					
No. of species 124;					
Principal species,					
Latrutes fucorum	0	0	0	+	0
Periclimenes americanus	+	+	+	+	0
P. iridescens	+	+	+	+	+
Hippolyte zostericola	0	+	+	+	0
Trachypeneopsis mobilispinus	0	0	0	+	0

Continued

TABLE II (Concluded)

	Shallow Sediment Community	Organic Sediment Community	Deep Lagoon Community	Pre-Reef Plain Community	Back-Reef Community
ARTHROPODA					
Thor paschalis	+	+	+	+	0
Tozeuma carolinensi	0	0	+	+	0
Panulirus argus	+	+	+	+	+
Clibanarius vittatus	0	0	0	+	+
Dromidia antillensis	+	0	0	+	0
Mithrax caribbaeus	0	0	0	+	0
Achelous ordawiyi	+	0	0	+	0
Squillid	+	+	+	+	+
Mysid sp.	+	+	+	+	0
ECHINODERMATA					
No. of species 35;					
Principal species,					
Oreaster reticulates	+	+	0	+	+
Ophioderma brevispinum	+	+	0	+	0
Lytechinus variegatus	+	+	+	+	0
Diadema antillarum	0	0	0	+	+
Clypeaster rosaceus	+	0	0	+	0
Meoma ventricosa	0	0	0	+	0
Isostichopus bandionotus	+	+	+	+	0
CHAETOGNATHA					
Spadella sp.	+	+	+	+	0
CHORDATA					
Ascidians					
No. of species 14;					
Principal species,					
Molgular occidentalis	+	+	+	+	0
Cephalochordata					
Branchiostoma caribaeum	0	0	0	0	+
Fish					
No. of species 98					
Others					
No. of species 23					

+ = present

0 = absent

These species were found to occur in five distinct communities (Fig. 2):

1. The shallow sediment community
2. The organic sediment community
3. The deep lagoon community
4. The pre-reef plain community
5. The back-reef community

Roberts (1971) recognized four communities, a division with which this study basically agrees, Table III, except insofar as we divide his largest community, the grass plain into two distinct zones - the deep lagoon and pre-reef plain.

4.1 The Shallow Sediment Community

This environment is found along the southern and western fringe of North Sound, where sediments are thin or absent. The fine carbonaceous sediments are typically 1-6 m deep, although greater deposits can be found. Water depth is between 1-2.5 m and water clarity is characterized by Secchi disc values of between 6 and 9 m.

The seagrass *Thalassia festudinum* is common to most of the area, showing good growth in sediment pockets but becoming stunted in the shallow sediments where there is little rooting medium. In sediment pockets typical leaf densities and average leaf lengths are 720 blades m^2 and 5 cm respectively. The leaves support a rich epibiont community.

Macro-algae are common on the thinner sediments and in the shallow waters, but become sparse in the dense *Thalassia* stands. A total of 35 Chlorophyta, 4 Phaeophyta and 22 Rhodophyta have been identified from this area (Table V), the dominant species being psammophytic chlorophyta such as *Avrainvillea nigricans*, *Halimeda incrassata*, *H. monile*, *Penicillus capitatus* and *P. lamourouxii*, which are replaced by species such as *Acetabularia crenulata*, *Cladophoropsis membranica*, *Dictyosphaeria cavernosa* and *Dasycladus* in the bedrock regions.

The most indicative members of this community are the turbidity-tolerant stony corals, principally *Siderastrea radians*, *Porites divaricata* and, to a lesser extent, *Favia fragrum* and *Porites asteroides*. These species rely upon a relatively firm substrate for colonization and are intolerant of deep soft sediments. The rocky substrate also permits establishment of alcyonarian species such as *Plexaura* and numerous sponges, including the giant loggerhead sponge, *Spheciospongia*.

The grazing gastropod population is sparse with only *Cerithium eburneum* present in any numbers. Species such as *Turbo castaneus*, *Tegula fasciata* and *Modulus modulus* so common in other parts of the Sound, are rare or absent in this locality. One environmental factor governing their distribution is thought to be the quantity of *Thalassia* leaf and associated epibiont community on which they mainly feed.

The burrowing bivalve population is restricted by the general paucity of sediments. Attached bivalves such as *Arcopsis adamsi* and *Barbatia* are a common feature of this environment, occurring wherever there is a suitable substrate for their attachment.

The caridean shrimps, such as *Periclimenes* and *Thor*, have low densities and, like the grazing gastropods, appear to be limited by the sparsity of *Thalassia* for food and shelter.

The sea urchin *Lytechinus variegatus* had densities of $1/\mathrm{m}^2$ over wide areas of this community. It is well known as the major consumer of *Thalassia* in most Caribbean areas (Moore *et al.*, 1963; Greenway, 1973) and observations made during this survey on its feeding habits showed it to be a voracious herbivore, feeding off both macro-algae and *Thalassia*.

TABLE III

A comparison of the community divisions described by Roberts (1971) with those of this study

This study	Roberts (1971)
Shallow sediment community	Shore zone
Organic sediment community	Restricted lagoon
Deep lagoon community, pre-reef plain community	Grass plain
Back-reef community	Reef shoal

TABLE IV

Total population dry leaves (data at different areas taken from Buesa, 1974)

Area	Density (g/m^2)	Author
Texas	373 (n = 12)	Odum, 1963
Tarpon springs to Apalachee Bay, Fla.	700	Bauersfeld *et al.*, 1969
Boca Ciega, Fla.	32 ± 3	Pomeroy, 1960
	480	Taylor *et al.*, 1973
Veracruz, Mexico (sheltered)	353	Los-Helgueras, 1971
Diego Perez Bay, Cuba (sheltered)	340	Buesa, 1972
Northwestern shelf (unsheltered)	76 ± 7 (0.1 – 1 154)	Buesa, 1974
Playa Habana (sheltered)	340 ± 50	Buesa, 1972
	517 ± 180	Buesa, 1974
Cayuelo, Cucana and S. Felipe (Southwestern Cuban shelf)(unsheltered)	80 ± 15	Buesa, 1972
Grand Cayman, North Sound	Average 92 Maximum 280	this paper

TABLE V

A comparison of the total number of species of Chlorophyta, Phaeophyta and Rhodophyta found in different areas of North and Little Sound

	Community				
	Shallow Sediment	Organic Sediment	Deep Lagoon	Pre-Reef Plain	Back-Reef
Chlorophyta	35	15	07	19	20
Phaeophyta	04	00	00	06	14
Rhodophyta	22	02	01	22	31

One particularly interesting feature of the shallow sediment community area is the presence of several geological anomalies in the form of holes and rock outcrops. These holes generally have small openings, rarely in excess of 50 cm, but it is in association with these faults that the greatest concentrations of *Panulirus argus* and fish such as *Lutjanus griseus*, *Lutjanus analis*, *Lutjanus joco* and *Pomocanthus paru* are found.

4.2 Organic Sediment Community

Little Sound and the eastern shore of North Sound were designated as the organic sediment community. The most notable feature of this environment is the deep organic sediment, for the most part derived from the adjacent mangroves. Water depths are typically 2-3 m and the water clarity low, with average horizontal Secchi disc values of 5-6 m.

These sheltered organic substrates support luxuriant stands of *Thalassia*, the rhizomes penetrating up to 30 cm into the substrate. Leaf densities and lengths as high as 750 blades m^2 and 70 cm were found. The epibionts, so characteristic of the shallow sediment community, were absent from the leaves in this area.

Algal diversity is generally low in this region and a total of 15 Chlorophyta and 2 Rhodophyta were identified. The dominant species are psammophytic Chlorophyta such as *Caulerpa ashmeadii*, *C. paspaloides*, *Halimeda incrassata* and *H. monile*. These algae can form large standing crops within limited areas and their individual size was greater than observed elsewhere in the Island waters. The rhodophyte *Coelarthrum albertisii* is characteristic of this region, being epiphytic on the, otherwise clean, *Thalassia* leaves.

The dominance of the flora by *Thalassia* and the lack of epibionts and algae doubtless account for the low gastropod numbers. Densities of the sea urchin *Lytechinus variegatus* were high, reaching 2 individuals/m^2.

The most distinctive species found in this area is the jellyfish *Cassiopea xamachana*. These scyphozoans were found close to the mangrove fringe in the sheltered waters, and in regions where *Thalassia* is absent; they reach densities as high as 20/m^2.

No detailed infaunal studies were made in this region, but a large bivalve assemblage is expected to be present.

4.3 Deep Lagoon Community

The south central part of the Sound is the deepest region with average depths of 4.5-6 m and a maximum of 9 m. Sediments are deep (50^+ cm) and of fine marl. Turbidity is substantially higher than elsewhere in the Sound (Secchi disc readings were always below 6 m) and this, coupled with increased water depth, results in a reduction of light incident on the bottom.

The area is dominated by large stands of *Thalassia*, but where the water depths exceed 5.5 m, the *Thalassia* is unable to grow and is replaced by *Syringodium filiforme*, which dominates to a depth range of 6.0 m. Below this depth macro-flora is limited to *Penicillus lamourouxii* and *Halimeda incrassata* on the marl bottom and to *Amphiroa fragilissima* on bedrock outcrops. In the shallow regions the *Thalassia* stands are, however, well established, the rhizomes penetrating up to 30 cm into the sediments. Leaf densities are typically 800 blades m^2 and average leaf lengths 25 cm, but epibiont communities on the leaves are few.

Algae in this region were uncommon and limited to psammophytic Chlorophyta such as *Avrainvillea nigricans*, *Halimeda incrassata*, *H. monile*, *Penicillus lamourouxii* and *Rhipocephalus phoenix*.

Overall, this deep grass plain has a very restricted epifauna due to the soft sediment and the limited growth of algae and epibionts. Few, if any, *Lytechinus* are present and the gastropod population is also low, although old thick-shelled conch, *Strombus gigas*, are found in the deeper waters where Thalassia is absent. There is a marked increase in the numbers of caridean shrimp, which can be related perhaps to the increased cover offered by the Thalassia.

Dominant macro-organisms are the burrowing bivalves, forming 88-94 percent by numbers of the total population. Two species constitute the bulk of these percentages, Ctena orbiculata and Anodontia alba. Anodontia appears to prefer the softer sediments; average densities of $78/m^2$ found in this region correspond well with figures of $77/m^2$ quoted by Moore and Lopez (1972) in Florida. Ctena was found throughout the Sound and appears to have a greater tolerance to different sediment types than does Anodontia.

Polychaetes accounted for 7-12 percent of the population by numbers whilst the crustaceans totalled 3 percent.

4.4 Pre-Reef Plain Community

North of the deep lagoon community a richer and more varied biota becomes established. Water depth decreases to 2.5-3.5 m and the sediments become coarser and more consolidated. Water clarity improves, there being greater exchange with the oceanic waters, and Secchi disc readings were, typically, between 7 and 10^+ m.

Thalassia testudinum still forms the major component of the flora, but its dominance decreases as the back reef zone is approached. Here, the angiosperm Syringodium filiforme becomes established. The epibiont communities are abundant on the Thalassia leaves and the melobesoid algae often totally cover blades, causing premature breakage.

Macro-algae are diverse and common, 19 Chlorophyta, 6 Phaeophyta, and 21 Rhodophyta being identified. The presence of more consolidated sediments, with shell and coral debris, provide good substrates for lithophytic species and the sediments are deep enough for psammophytic types.

Unlike the deep lagoon community, the pre-reef plain supports a flourishing epifaunal assemblage, the most obvious members of which are the sea urchins. The principal echinoderm is Lytechinus variegatus, occurring here with a maximum density of $2/m^2$, a value which compares with average densities of $1.9/m^2$ in Biscayne Bay, Florida (Moore et al., 1963), and densities of $20/m^2$ in parts of Jamaica (Greenway, pers. comm.). The reason for this great disparity with the latter figure might be due to the difference in Thalassia standing crop, 80-100 g dry weight leaf/m^2 for Jamaica and 24 g dry weight leaf/m^2 pre-reef plain North Sound. The tendency for the urchins to aggregate, as reported by Moore et al., was observed also in North Sound.

Clypeaster rosaceus was the other main echinoderm found in this region. Its distribution is more restricted than Lytechinus and, at maximum densities, does not exceed $1/m^2$. It can be found in small concentrations in the "shallow sediment community" but is principally restricted to this area. Meoma ventricosa occupies a limited portion of the "pre-reef plain" but the true size of the population is hard to estimate due to its burrowing nature. The two urchins Tripneustes esculentus and Diadema antillarum, more commonly found in shallow reef areas, were observed occasionally in this region.

The firmer substrate and clearer water encourages the growth of a variety of sponges, especially the small green sponge Haliclona viridis, but the difficulties encountered in identifying this group have precluded positive identification of all species found within North Sound.

The gastropod population reached its highest densities in this region with Turbo castaneus, Modulus modulus, Tegula fasciata, Cerithium eburneum, C. literatum and Astraea phoebia being the most common species. The gastropod grazing population rose from 1.4 percent by numbers of the total population in the deep lagoon community to between 11-21 percent in this sector. This notable increase in grazing molluscs can be correlated with the increased epibiont communities on the *Thalassia* leaf and other substrates, but the densities are lower than similar areas of Biscayne Bay (Brook, 1975). This is probably due, as was thought the case with *Lytechinus*, to the lower *Thalassia* standing crop.

Polychaete numbers were down to between 3-5 percent of the total population but the bivalves retained their dominance, representing 68-91 percent by numbers of invertebrate population. The vast majority of the bivalves were *Ctena orbiculata* with densities reaching 233/m^2.

4.5 The Back-Reef Community

This community is arbitrarily defined as being in the area extending from the reef crest to the stands of *Syringodium* and *Thalassia* of the pre-reef plain. Biologically it is diverse and encompasses a complex series of habitats, individually related to the seabed character. The latter consists of a variety of substrata, including sand, rubble, bedrock and coral. The water, depth ranging to 5 m, tends to be oceanic and clear.

Typically this area is devoid of marine angiosperms, but a few isolated patches of *Thalassia* and *Syringodium* are present in sediment pockets.

A total of 20 Chlorophyta, 14 Phaeophyta and 30 Rhodophyta have been identified from this region. The Phaeophyta form the major floral biomass of most areas, especially the genera *Pocockiella* and *Dictyota*. These algae are found attached to bedrock, rubble and shell debris. Sand areas of this region are colonized by psammophytic species such as *Halimeda incrassata*, *H. monile*, *Udotea flabellum*, *Penicillus capitatus* and monofilament species such as *Chaetomorpha nodosa*. The Rhodophyta can be common, species such as *Acanthophora spicifera* and *Hypnea musciformes* tending to grow on coral and shell debris while *Amphiroa fragilissima* and *Jania* sp. are found in crevices and as parts of general algal mats.

The epifauna was very different from that found elsewhere in the Sound. Bedrock areas supported numerous colonies of stony corals, including *Isophyllia sinuosa*, *Montastrea annularis* and *Diploria strigosa*. The variety of corals in this region is far greater than the bedrock areas of the shallow sediment communities, this due no doubt to the reduction of particulate matter in the water. Large stands of *Plexaura homalla* and a wide variety of sponges are common. Rubble areas contained populations of squillid and alphaeid shrimps as well as attached bivalves, e.g., *Lima*. Sand regions had a restricted epifauna except for the cushion star *Oreaster reticulatus* and large gastropods such as *Strombus gigas*, *Cassis tuberosa* and *Charonia variegata*; these three gastropods tended to be uncommon due to overfishing.

Infauna is severely restricted in the shallow sand deposits and no clear species dominance was indicated. *Ctena orbiculata* is present, but in fewer numbers than found elsewhere. Tellins are more abundant here than in other parts of the Sound and a population of the cephalochordate *Branchiostoma caribaeum* is present.

Surveys of deeper sand deposits, where banks have been formed, showed an even further reduction of infauna. On the sand-banks lacking vegetation only a few tubiculous polychaetes and burrowing shrimp were present, whilst sand-banks being consolidated by the seagrass *Syringodium filiforme* had the same, plus a few bivalves. The small infauna population of these areas is thought to be due to the banks' proximity to the surface, resulting in instability of the sand.

4.6 Fish Populations

The fish population was fairly well distributed across the various bottom communities except where bottom anomalies and reefs occur, resulting in aggregation of fish. The most common fish occurring in the Sound is *Monocanthus aliatus*, an omnivore feeding mainly on copepods and ostracods. Other common species were *Paraclinus fasciatus*, *Malacoctenus triangulatus* and *Sparisoma radians*. The fish population in the back-reef community is somewhat higher than in the rest of the Sound, 132 as opposed to 98 species being reported here.

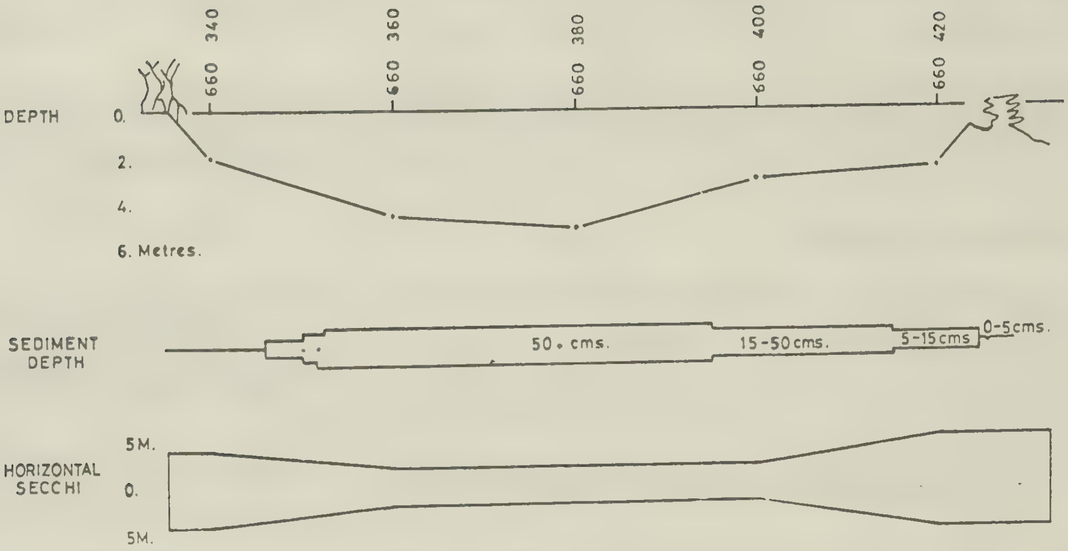
660 340
660 360
660 380
660 400
660 420
DEPTH
0.
2.
4.
6. Metres.
SEDIMENT DEPTH
50. cms.
15-50cms.
5-15cms
0-5cms.
HORIZONTAL SECCHI
5M.
0.
5M.

Fig. 3 Transect across North Sound illustrating water depth, sediment depth and water clarity

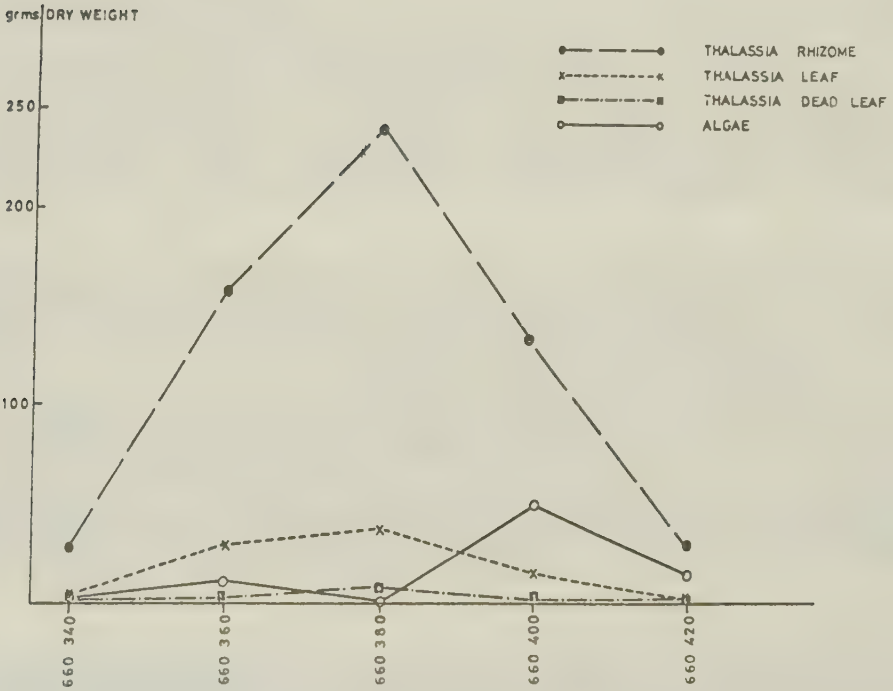

Fig. 4 Transect across North Sound showing typical flora biomass during April 1975

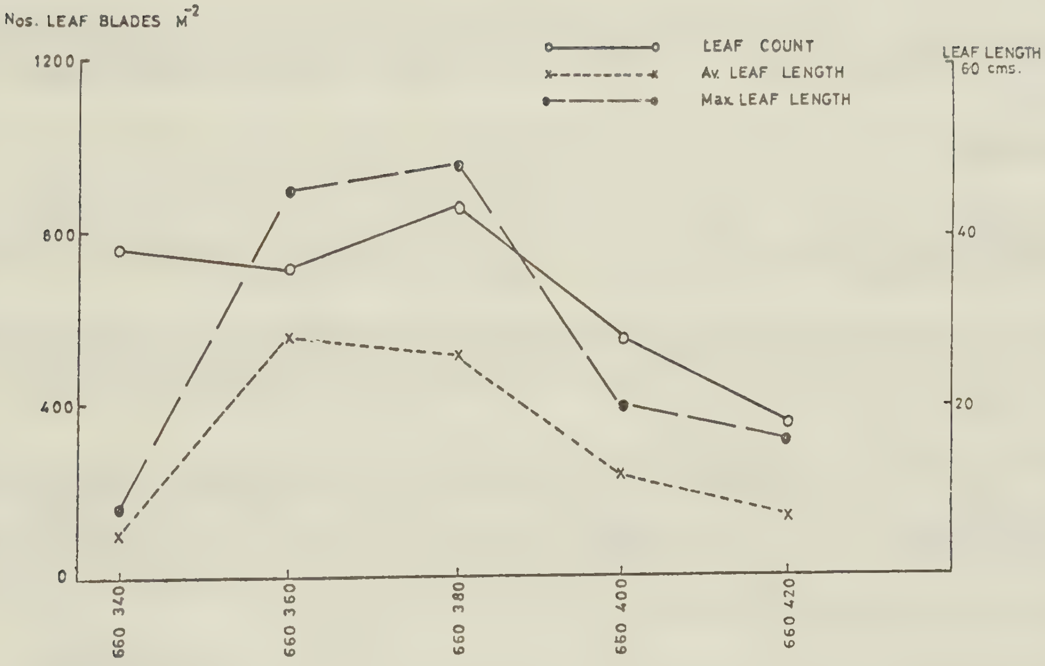

Fig. 5 Transect across North Sound showing typical Thalassia leaf densities and average and maximum leaf lengths during April 1975

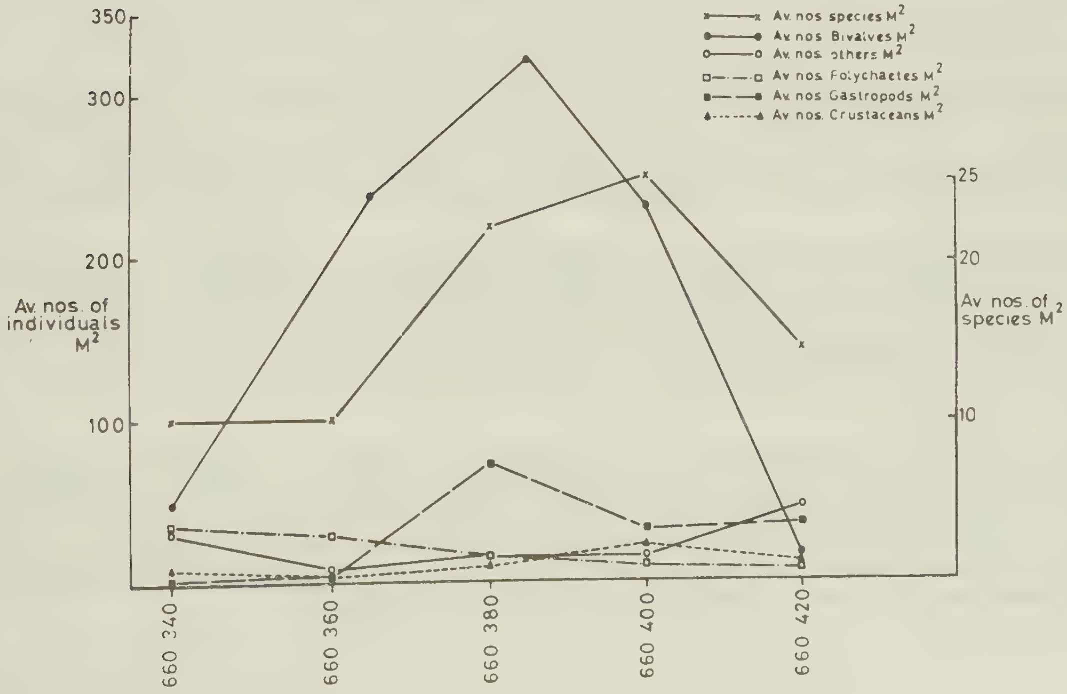

Fig. 6 Transect across North Sound showing typical species numbers and animal numbers during April 1975

4.7 Suction Pump Transect

Results obtained from the survey utilizing the Venturi-type suction pump provide more specific quantitative data (Figs. 3, 4, 5 and 6). They also show more clearly the relationship between environment (Fig. 3) flora biomass (Figs. 4 and 5) and animal numbers and diversity (Fig. 6).

5. DISCUSSION

North Sound comprises a complex and varied benthic community. The distribution of different species is related to physical parameters such as water depth and clarity, and sediment depth and composition.

The dominant biological feature of the area is the turtle grass *Thalassia testudinum*, which grows in over 9/10 of the Sound. Its density varies for each community but, even the maximum standing crops measured, appear to be lower than found in other areas of the Caribbean (Buesa, 1973) (Table IV).

The importance of *Thalassia* leaves as a substrate for epibiont communities has been reported by Humm (1968) and observations made in North Sound support this claim. Epibiont cover on the leaves varies in each community, greatest numbers being found on the *Thalassia* of the pre-reef plain. Epibionts form an important food source, especially for the grazing gastropods, and there appears to be strong correlation between the quantity of available epibionts and the gastropod populations.

Macro-algae also display differences in their distribution in the communities (Table IV). Turtle grass stands exclude all but psammophytes such as *Halimeda incrassata*, *H. monile* and *Penicillus* sp. whilst the bedrock rubble and shallow sediment areas are able to support a more diverse flora.

The greatest density of invertebrates found in the Sound was 438 individuals/m^2 in the grass plains at the southern part of the pre-reef plain, with a clear dominance by the bivalve *Ctena orbiculata*. However densities, usually, were lower than this (Fig. 6).

Seasonal variations in the Sound were only obvious by the breeding seasons of certain species, especially the spiny lobster and the sea urchin *Lytechinus*. Such breeding seasons tended to be longer than those reported from further north in Florida and Bermuda and shorter than those of areas south of Cayman, such as Antigua, where an all-year-round breeding season is suggested (Peacock, 1974). However, there was strong evidence on Cayman that a few species at least, e.g., the caridean *Periclimenes tridescens*, have a continual breeding season.

In conclusion, the communities of North Sound appear to represent a variety of ecological systems ranging from the high species diversity and low individual numbers of the bedrock, rubble and thin sediment areas to the higher individual numbers and lower species diversity of the *Thalassia* stands and the deep sediment areas.

6. ACKNOWLEDGMENTS

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THE SABA BANK - A LARGE ATOLL IN THE NORTHEASTERN CARIBBEAN

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Abstract

The Saba Bank is a rather large submerged island in the northeastern Caribbean. Its top is remarkably flat, the water depth being about 20 to 40 m over most of its surface. There are several peripheral reefs around the whole bank and because of this it may be called an atoll, even though on some of these reefs there is probably no modern coral growth. The presence and distribution of shallow water stony corals in the area is discussed in some detail. As an atoll the Saba Bank is remarkable for its very large surface area, the great height of most of its Holocene reefs and the exceptional width of its windward reef flats.

Resumen

El Banco de Saba es una isla sumergida, de extensión bastante grande, situada en el nordeste del Caribe. Su parte superior es notablemente llana y en la mayoría de su profundidad del agua es de 20 a 40 m. Alrededor del banco existen varios arrecifes periféricos, por lo que puede considerarse un atolón, aunque probablemente en algunos de esos arrecifes no se registran crecimientos modernos de coral. Se examina con cierto detalle la presencia y distribución de los corales pétreos de aguas poco profundas. Entre los atolones, el Banco de Saba destaca por la extensión de su superficie, la gran altura de la mayoría de sus arrecifes holocenos y la anchura excepcional de la plataforma de arrecife de barlovento.

1. INTRODUCTION

Most Dutch institutes involved in the CICAR programme, including the Rijksmuseum van Natuurlijke Historie (National Museum of Natural History), concentrated their efforts on two areas, the Guyana region and an area near the Windward Islands of St. Martin, St. Eustatius and Saba, including the Saba Bank. The latter area was visited several times in 1972 by the hydrographic vessel H.NL.M.S. LUYMES, primarily to carry out bathymetric surveys. However, most of the cruises were partly, or even mainly, devoted to sedimentological, geomorphological and biological investigations. Unfortunately, physical and chemical oceanography could not be included in this part of our national programme.

Some results of our bathymetric, sedimentological and biological work on the Saba Bank are presented in this paper. A popular account of this work was given by Roessler (1974). The bathymetric survey was carried out by Commandant L.H. van Opstal, hydrographer of the Dutch Navy, and several of his officers. The results of their work, as well as the original echograms, were kindly put at my disposal by the Hydrographic Office in The Hague. The unusually accurate bathymetric survey of this area in the open sea was possible only because a Seafix navigation chain had been established on the three islands mentioned above. Part of the bathymetric work had been done already when we started our sedimentological and biological programme, but the morphology of some important areas was still unknown; consequently the station network did not cover some areas we would have liked to study.

Between 12 May and 17 June 1972 about 130 sedimentological and biological stations were made in the whole area; most are indicated on the map (Fig. 1). Because SCUBA diving proved to be the most important method for studying the structure and fauna of the Saba Bank, the diving stations have been specially indicated and numbered. The other stations include grab, dredge and trawl stations.

2. GENERAL SURVEY OF THE AREA

The Saba Bank proper is a roughly rectangular bank west of the islands of Saba and St. Eustatius. It is 60-65 km long, 30-40 km wide and has a surface area of 2 000 km^2. Water depth is 20-40 m over most of the bank. Its surface slopes very gradually from the shallower southeastern part to the deeper northwestern part. Due to the small differences in depth a bathymetrical chart cannot be made easily; moreover, on a small scale, it would not show the information we wish to present. I preferred, therefore, to compile a structural map (see Fig. 2) showing only geomorphological details other than flat bottom and more or less gradual slopes, *viz.* reefs and escarpments. Reefs are defined here purely as morphological entities, i.e., as structures arising from the surface of the bank. In contrast to the rest of the bank, practically always they show a very irregular profile in the echograms. The reefs along the flanks of the bank always have a very steep, and mostly very high, seaward slope. The lagoonward limits of these reefs also are very often definite escarpments but, in some areas, they slope gradually, more or less, toward the lagoon floor. The escarpments indicated on the map are not associated with significant reef formations.

North of the Saba Bank there is a seamount which, for convenience, we called Luymes Bank. It has an extremely intricate structure, with several tops at depths between 73 and 80 m and is connected to the Saba Bank by a ridge having a minimum depth of about 90 m. It has been suggested that the Luymes Bank originated as a volcano belonging to the volcanic arc of Nevis, St. Kitts, St. Eustatius and Saba (Westermann and Kiel, 1961: p. 166-167). This might well be the case, but nowadays the area is covered completely by carbonate rocks and sediments.

Fishermen on Saba told Boeke (1907: p. 45), one of the first authors to give a reasonably accurate description of the Saba Bank, there was a shallow area which they called Copper Bank, close to the Saba Bank, at 8-10 miles SSE of Saba. They did not fish on that bank as they believed fish from the area were always poisonous (apparently causing ciguatera). It is now evident that the Saba fishermen referred to the "peninsula" opposite St. Eustatius (see Fig. 1) and not to a separate bank.

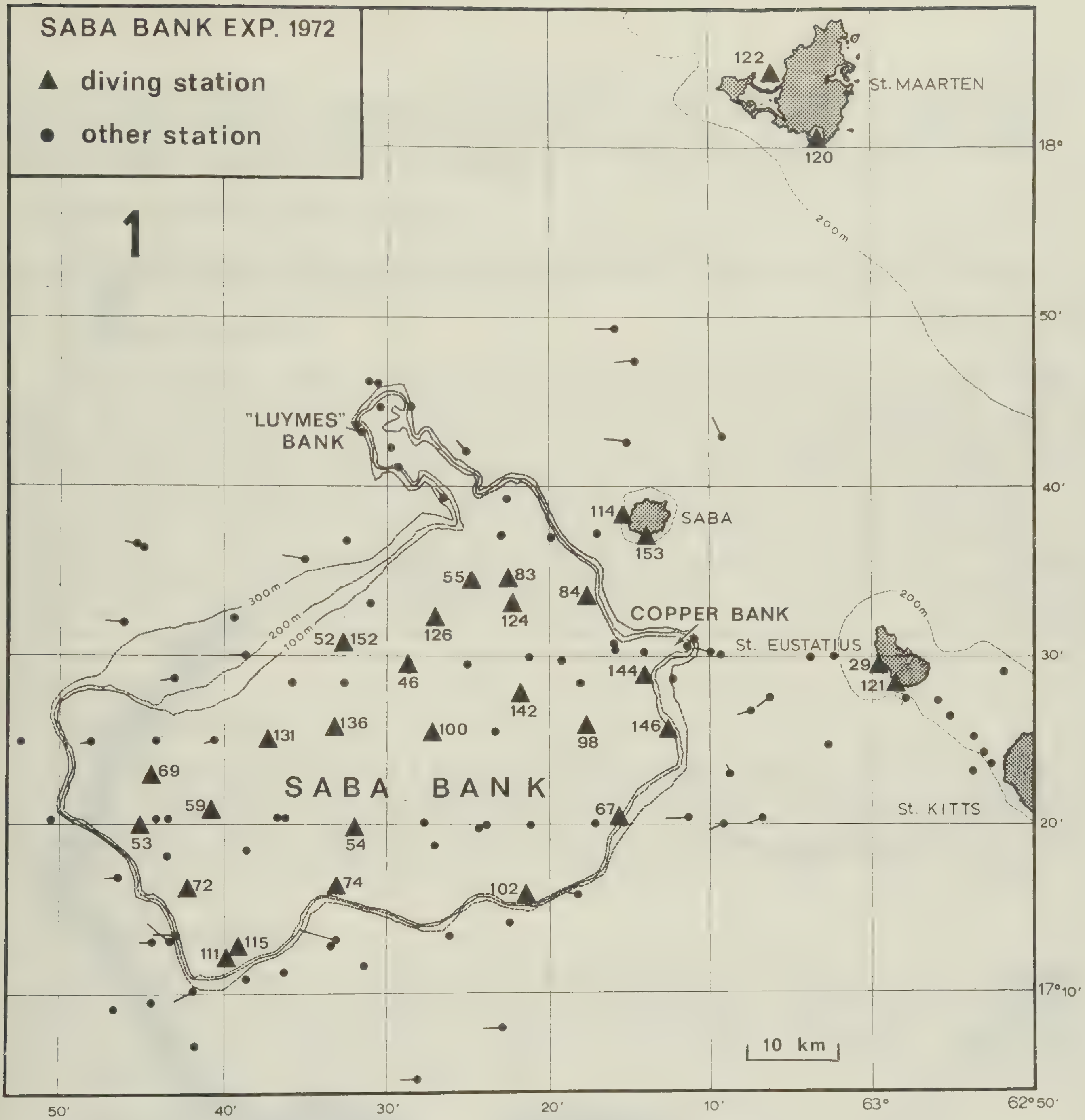
SABA BANK EXP. 1972
▲ diving station
● other station
1
122
St. MAARTEN
120
18°
200m
50'
"LUYMES" BANK
40'
114
SABA
153
55
83
84
124
126
300m
200m
100m
52
152
COPPER BANK
St. EUSTATIUS
200m
29
121
30'
46
144
142
136
131
100
98
146
69
SABA BANK
59
53
54
67
St. KITTS
20'
72
74
102
111
115
17°10'
10 km
50'
40'
30'
20'
10'
63°
62°50'

Fig. 1 Map with stations of the LUYMES Saba Bank Expedition of May to June 1972. The numbers refer to the diving stations only

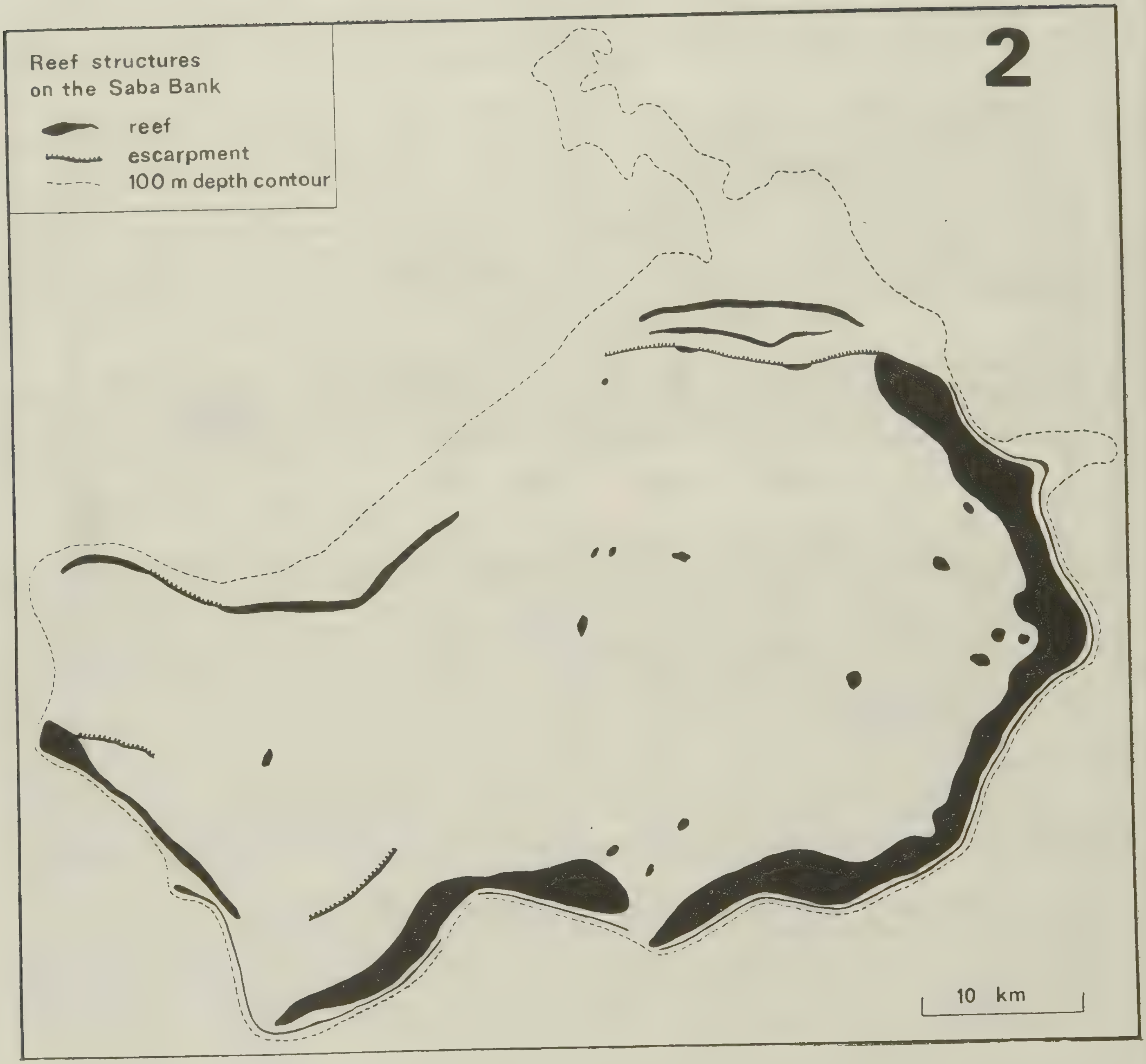
Reef structures
on the Saba Bank
reef
escarpment
100 m depth contour
2
10 km

Fig. 2 Map of the Saba Bank indicating reef structures found during bathymetric surveys by H.NL.M.S. LUYMES in 1972

So far as I know, the currents in the area run in a WNW direction constantly throughout the year and, usually, the wind direction varies only between E and ESE. In general the current is not very strong, but we observed a relatively strong current over the shallow windward reefs, which is quite understandable.

3. DESCRIPTION OF THE REEF STRUCTURES

A rough description of all reef structures as defined before, and based exclusively on the the echo soundings, is given below.

3.1 The Southeastern Reef

This semicircular reef, running along the eastern and part of the southern edge is, by far, the largest reef on the Saba Bank. Its total length is about 55 km and its width varies from 1 to 3 km (in some places it widens to 3.5-4 km). Over the whole length of the reef the minimum water depth varies from 12.5 to 16 m. This means the reef rises to a maximum height of 6-9 m above the lagoon floor, which floor lies at a depth of 19.5-23 m on this part of the bank. Along the greater part of its length there is a distinct, 2-4 m high, escarpment on the lagoonward side of the reef, but in some areas the reef slopes gradually down to the lagoon floor. In most areas the reef has a very irregular surface morphology, as shown by numerous sharp peaks on the echograms but, in places, its surface is rather flat. In general the highest parts of the reef lie close to the seaward slope. Often one can distinguish an outer reef flat and an inner reef flat, the latter being a few metres lower. The reef front is invariably very steep, sloping down to a terrace which lies usually at a depth of 21-30 m, sometimes at a depth of about 40 m. This means the slope is mostly 7-15 m, sometimes up to 25 m high.

3.2 The Southern Reef

This second largest reef has a length of about 25 km and varies in width from 1.5 to 3 km. It looks very much like the SE reef but, in general, lies at a slightly lower level. On this part of the bank the lagoon floor is at a depth of 27-30 m, while the highest points of the reef reach up to depths varying from 15 to 24 m. This means this reef has a maximum height of 8-12 m above the lagoon floor and is consequently, on average, somewhat higher than the SE reef.

3.3 The Southwestern Reef

This reef is about 17 km long, about 1.5 km at its widest, but only 300-500 m wide over most of its length. This reef, again, lies at a lower level than the preceding one. The lagoon floor lies at a depth of 40-44 m, while the minimum depth over the reef varies between 30 and 40 m. The reef height above the lagoon floor varies from a few metres to 10 m. There is a seaward terrace at a level of about 40 m.

3.4 The Northwestern Reef

This structure, overall, is about 25 km long, but no significant reef formations are present over 4.5 km of this length. Its width could not be measured accurately, but is in the order of 200 m. In this area the lagoon floor slopes in a westerly direction from 41 m to a depth of 53 m, at the same time the minimum water depth over the reef decreasing from 34 to 43 m. Maximum height of the reef relative to the lagoon floor varies between 4 and 10 m. Between the two parts the line of the reef can only be followed as an escarpment with a height of about 3 m. There is a steep seaward slope 10-20 m high passing into a more gradual slope; a distinct terrace is lacking here.

3.5 The Northern Reefs

The northern part of the Saba Bank, facing the Luymes Bank, is exceptional in that, here, a series of three reefs on different levels can be recognized. The first, lagoonward reef, which could well be considered a continuation of the SE reef, is not much more than an escarpment with a few reef patches (probably rather more than the two indicated on the map). It is about 16 km long. The top of the escarpment slopes from 21 m deep in the east to 39 m deep at its western end, while the terrace at its bottom lies at a depth of 30-41 m. It is between 3 and 9 m high, depending partly on the presence or absence of a reef.

The second reef is considerably shorter but appears to be continuous. It is situated on the edge of a terrace sloping in a westerly direction from 41 to 52 m water depth. The highest tops of the reef are about 30 m deep at the eastern to 45 m deep at the western end. Maximum height relative to the level of the terrace varies from 7 to 12 m.

The third, seaward reef, is on a sloping terrace 42-58 m deep; its highest tops are at depths of 33-47 m while its maximum height varies from 7 to 11 m.

3.6 The Patch Reefs

As indicated on the map, at least 15 patch reefs were found in the lagoon but we can be sure their real number is considerably higher. Due to their small size, most of them must have been missed during the soundings. On the echograms they stand out as conspicuous structures on the flat lagoon floor. Their height varies from 2 to 6 m but most are about 4 m high. Most patch reefs were encountered on the eastern half of the bank, where the lagoon floor is 20-29 m deep. On the western half of the bank only one patch reef was found at a depth of 36 m.

3.7 The Front Reefs

One of the most remarkable features of the Saba Bank is the presence of a narrow ridge in front of some reefs mentioned before, along practically the whole length of the eastern and southern "coasts". Usually the base of the front reef occupies most of the narrow terrace which is present everywhere in this area and which is 100-500 m wide (only in some places it is up to 1 000 m wide). The reef top in front of the SE reef lies 21-28 m below sea level in its northern half and 14-20 m below sea level in its southern half. As mentioned above, the terrace in this area is 21-30 m deep, sometimes even 40 m deep. In some places the front reef is so low as to be varely visible on the echograms. Mostly it has a considerable height, up to 15 m, in some places even up to 20 m, which means that it is higher than any of the other reefs on the Saba Bank.

The rim in front of the south reef is somewhat smaller and even lacking in the central part but along most of its length it is still 4-9 m high (the rim lies on a terrace at a depth of 24-33 m while its top lies 19-26 m below sea level).

In the area where the western parts of the front reef are situated the number and the quality of the bathymetric observations do not allow us to give an exact description. Between the south reef and the southwestern reef the rim is certainly not very high and probably not continuous. As indicated on the map, the western extremity is situated on the edge of a terrace more than 1 km wide and about 42 m deep. Here the massive front reef rises to 14 m above the terrace level.

It should be noted that the terrace on which the front reefs are situated lies at the same depth as the lagoon floor in the same area in most places, or only a little lower.

4. THE SHALLOW-WATER STONY CORALS

Numerous zoological specimens and samples were collected in the area. All material has been sorted in the museum sorting centre and several groups have been either worked up or are being studied. In this paper I have confined myself to the presentation of results obtained by a study of the shallow-water stony corals (Milleporina and Scleractinia) as these animals are most important for an understanding of the morphology of the area.

The qualitative results are summarized in Table I. Since I do not wish to enter into taxonomic and nomenclatorial discussions in this paper, and in order to avoid confusion, I adhered strictly to Roos' (1971) views on the taxonomy and nomenclature of these animals. This author undertook an extensive survey of the shallow-water stony corals of the Netherlands Antilles and the results of his work on St. Martin, Saba and St. Eustatius are particularly relevant to the present study. Bak (1975) contributed some valuable additional observations on the coral fauna of these islands. We only worked incidentally in coastal waters, the results being summarized in the last columns of Table I. We collected very few corals near St. Martin since we dived in only two of the sheltered bays.

It appeared that a rich coral fauna was present only on the two large windward reefs on the Saba bank, the southeast and the south. In this area we made eight diving stations, finding 22 coral species. Collecting methods were far from intensive so the number of species actually occurring is, no doubt, considerably higher. The main reason we can call this a rich coral reef is that the number of colonies per station is very high and large colonies are common. Moreover, the patches of sand and bare rock are usually small. It is evident that both reefs form an area with constructional coral growth. This is not the case with fore-reef stations numbers 111 and 146, where only small, scattered colonies were found. Sand patches and sediment rivers are common there.

Corals are common also on the first of the northern reefs (station 55) but the colonies are small and scattered, at least on the single station in this area. On the second reef a few corals only were found (station 83, 41 m) but the diving station was on one of the lowest parts of the reef.

On the lagoon diving stations, seven were made in the southeastern half of the lagoon (east of a line between the western ends of the series of north reefs and the south reef) at depths from 21 to 36 m. At two of these stations (numbers 54 and 98) there were no stony corals at all. At the other stations (see Table I, numbers 46 to 126) a total of 17 species was collected but in all cases there were small and scattered colonies with only an occasional coral head. Eight diving stations were made in the northwestern half of the lagoon at depths from 34 to 44 m. Only two small coral colonies of two species were found at two stations (see Table I, numbers 59 and 69).

The following general observations must be added here:

(a) Many reef areas in the Caribbean are dominated by one or a few species which form dense stands or huge colonies, sometimes to such an extent that definite reef communities can be distinguished, e.g., Montastrea annularis reef, Porites reef or Acropora cervicornis reef. On the Saba Bank this is nowhere the case. At none of the diving stations was the scene dominated by certain species and really large colonies were never found.

(b) Most coral species do not show a definite distribution pattern on the Saba Bank; the only exception is Acropora cervicornis, which was found only on the windward reefs, i.e., the southeast and the south reefs, at six stations (including three diving stations) and only in shallow water, from 15 to 24 m depth. The Acropora colonies were invariably very low and often streamlined.

(c) Only three species of scleractinians were found in the coastal waters but not on the Saba Bank, viz. Acropora palmata, Astrangia solitaria and Tubastraea tenuilamellosa. So far as I know all three are typically shallow water species which can hardly be expected to occur on the Saba Bank.

(d) Madracis asperula is the only species found in several localities on the Saba Bank but not in the coastal waters. Roos (1971) did not find this species in any of the many localities he visited along the coasts of the island of Saba, St. Eustatius and St. Martin. He has already stated, "this species is restricted to shallower parts of the open sea".

TABLE I

Stony corals (Milleporina and Scleractinia) collected at the diving stations

	Windward reefs								N reefs		Lagoon stations							Coastal waters		
Diving stations:	102	144	84	67	74	115	111	146	55	83	46	142	100	124	126	59	69	S	E	M☆
Depth in meters:	16	16	17	20	23	26	28	30	39	41	21	22	24	24	36	37	44	-20	-15	-15
Millepora squarrosa	·	★	★	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	★	·
Millepora alcicornis	★	★	★	★	★	★	★	★	·	·	·	·	·	★	·	·	·	★	·	·
Millepora complanata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	★	·	·
Stephanocoenia intersepta	·	·	★	·	★	·	★	★	★	★	·	·	★	·	·	·	·	★	·	·
Madracis asperula	·	★	·	★	★	·	★	·	★	·	·	·	·	·	·	·	·	·	·	·
Acropora cervicornis	·	★	★	★	·	·	·	·	·	·	·	·	·	·	·	·	·	★	★	·
Acropora palmata	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	★	★	★
Agaricia agaricites	★	★	★	·	★	·	★	★	★	·	★	·	·	★	·	·	·	★	★	·
Porites porites	★	★	★	★	·	★	·	★	·	·	·	·	·	·	·	·	·	★	·	★
Porites astreoides	★	★	★	★	·	★	·	★	·	·	·	·	·	★	·	·	·	★	·	·
Siderastrea radians	★	★	★	★	★	★	★	·	★	·	★	★	★	★	·	·	★	·	★	·
Montastrea annularis	·	·	·	★	★	·	★	·	★	·	·	·	·	·	·	·	·	★	★	·
Montastrea cavernosa	★	★	★	★	★	★	·	·	★	·	★	★	★	★	·	·	·	★	★	·
Solenastrea bournoni	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	★	·	·	·	·
Diploria clivosa	·	·	·	·	·	·	·	·	·	·	·	★	·	·	·	·	·	★	·	·
Diploria strigosa	·	·	★	★	★	·	·	·	·	·	·	·	★	★	·	·	·	★	★	·
Diploria labyrinthiformis	★	★	★	·	★	★	·	·	·	·	★		★	·	·	·	·	★	·	·
Manicina areolata	★	★	·	·	★	★	★	★	★	★	★	★	·	★	★	·	·	★	★	★
Colpophyllia natans	★	·	★	·	★	★	★	★	★	·	·	★	·	·	·	·	·	★	★	·
Astrangia solitaria	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	★	·	·
Dendrogyra cylindricus	·	★	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	★	·	·
Dichocoenia stokesii	★	★	★	·	★	★	★	★	·	·	★	·	★	·	·	·	·	★	★	★
Scolymia lacera	·	·	·	·	·	·	·	·	·	·	·	★	·	·	·	·	·	·	·	·
Mussa angulosa	·	★	·	★	★	·	·	·	★	·	·	·	★	★	·	·	·	·	★	·
Isophyllastrea rigida	·	·	·	·	·	·	★	·	·	·	★	★	·	·	·	·	·	★	★	·
Isophyllia sinuosa	·	★	★	·	★	★	★	·	·	·	·	·	·	★	·	·	·	★	★	★
Mycetophyllia lamarckana	·	★	·	·	★	·	·	★	★	·	·	·	·	·	·	·	·	★	★	·
Eusmilia fastigiata	★	★	·	·	★	·	·	★	·	★	·	·	·	★	·	·	·	·	★	·
Tubastraea tenuilamellosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	★	·	·
Number of species:	11	17	14	10	16	10	11	10	10	3	7	7	7	10	1	1	1	12	16	5
Total number of species:	22								11		18							26		

☆ S = Saba (stations 114, 153), E = St. Eustatius (station 121), M = St. Martin (stations 120, 122)

5. MISCELLANEOUS OBSERVATIONS

The fauna of the two large windward reefs is dominated by stony corals, but practically everywhere gorgonians are also very common. In some places they form dense stands of different species with but few stony corals in between. As in Acropora cervicornis, the branching colonies always remain relatively low and really large colonies, such as those commonly found in coastal waters, were never encountered.

In the eastern part of the lagoon, stony corals as well as gorgonians are usually present but they are nowhere dominant. In general the fauna is rather rich. In some places algae or sponges can be considered the dominant bottom organisms. In this area the bottom is usually rocky with stones and scattered (mostly dead) coral heads. Sand patches are quite common but the layer of sand is always very thin.

In the western part of the lagoon not only corals, including gorgonians, are virtually absent, but the rest of the fauna is also extremely poor. Most of this area is covered with sand and, in several places, sandwaves, possibly caused by hurricanes, could be recognized. Nevertheless, the layer of sediment is rather thin and probably never more than 10-20 cm thick. At most stations the area gave the impression of a desert to the divers and not many animals were encountered. At a few stations there was an algal vegetation of some significance. Although in general the bottom is sandy, trawling proved to be practically impossible because of the still rather numerous outcrops and boulders, as was also experienced by Boeke (1907: p. 145).

Probably much of the sandy sediment in the lagoon is produced by calcareous algae and, in several places, this is particularly evident because the sand particles can still be recognized as segments of Halimeda.

6. GENERAL CONCLUSIONS

It is to be regretted that several of the reef structures on the Saba Bank could not be studied, mainly because we were not aware of their existence when we started our expedition, partly because of technical difficulties and lack of time. However, we do know now that the two large windward reefs over most, or even all, their length carry such a rich reef fauna that reef building processes must be quite active there. We can be sure that structural coral growth occurs also to a greater or lesser extent on the first north reef, the front reefs and at least part of the patch reefs. We do not know anything about the fauna of the southwest, the northwest and the deeper north reefs, but we doubt very much that reef-building of any significance occurs there at the present time. Not only do they have a less favourable leeward position but they are also situated at a considerably greater depth than the other reefs. Moreover, the desert-like environment of the rest of the northwest half of the Saba Bank is not very promising.

7. THE ORIGIN OF THE SABA BANK

The Saba Bank undoubtedly has a volcanic base but, as yet, we have no information on this. We can only say that we did not find rocks of volcanic origin, but did find some black sand, presumably of volcanic origin, on the southwestern part of the Bank. At present its surface seems to consist almost completely of carbonate rock and carbonaceous sediments. Geologists believe that a composite volcanic island is buried under these more recent formations (Westermann and Kiel, 1961: p. 166).

One of the most puzzling aspects of the bank is that it has a remarkably flat top. Vaughan (1919: p. 320) has already written: "What the processes were that caused the levelling of the summits [of Saba, Pedro and Rosalind Banks] is a matter of pure speculation, but it seems probable that they were subaerial erosion and submarine planation". Davis (1926, p. 137-138) explained the flat top of the Saba Bank by considering it "an atoll-lagoon floor, deprived of its original reef and probably somewhat planed down by low-level abrasion in the last glacial epoch".

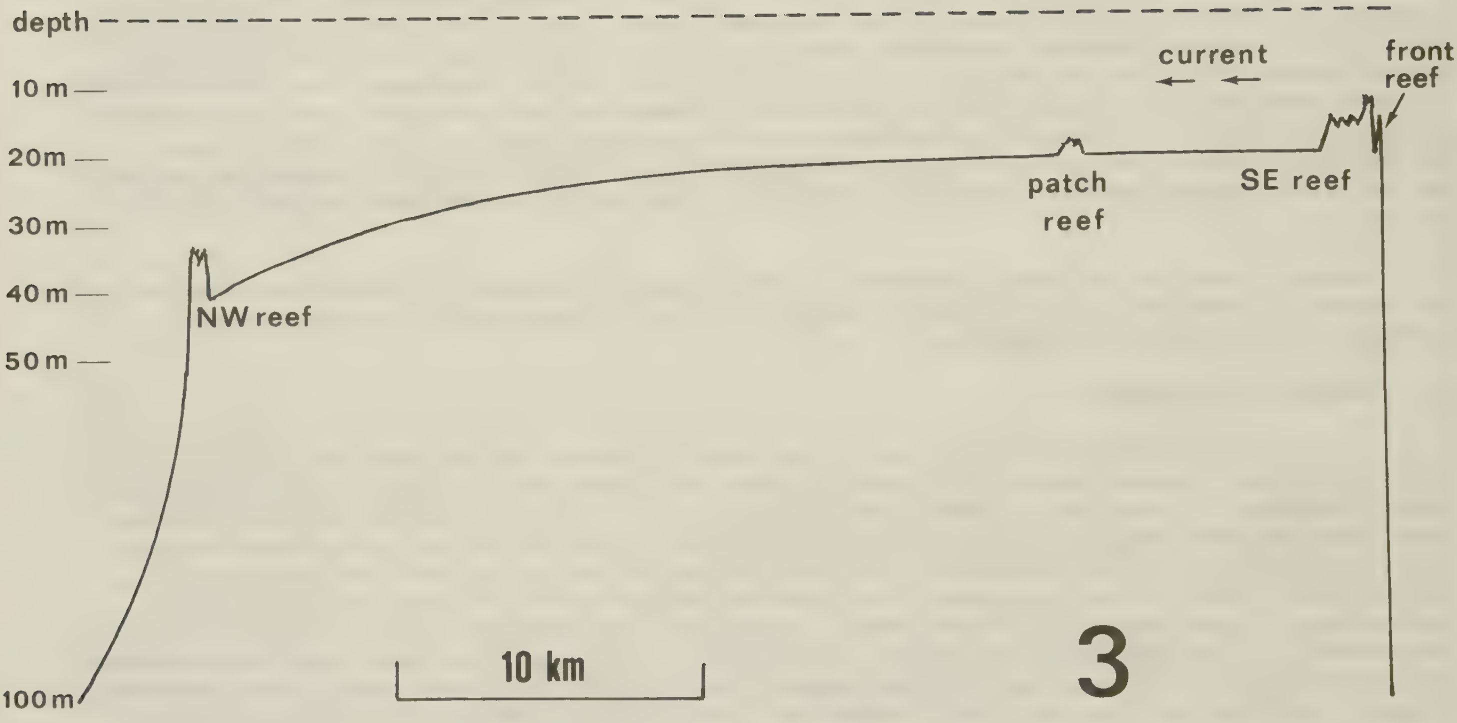
depth
10 m
20m
30m
40 m
50 m
100m
current
front reef
patch reef
SE reef
NW reef
10 km
3

Fig. 3 Diagrammatic cross-section of the Saba Bank in a direction WNW to ESE

Indeed, we can be sure that the Saba Bank was an island during the last glacial period until at least about 5 000 years ago, but it is remarkable that effects of subaerial erosion could not be found. On a former island if this size one expects to find at least some traces of rivers or gullies. It should parenthetically be remarked that all channels between the reefs lie at the same level as the adjoining lagoon floor. Consequently they cannot be considered drowned rivers or ravines. Perhaps the area was extremely dry during the last glacial epoch.

8. HOLOCENE DEVELOPMENTS

It is evident that all ridges described before must be considered reefs. Their quite irregular surface, their very steep slopes and their sharp summits indicate that they do not date back to the time when the Saba Bank was an island but that they were formed afterwards (Fig. 3).

So far as we know, luxuriant coral growth is restricted mainly to the two large windward reefs. It was not unexpected that only a meagre growth of reef corals was found on the rest of the bank since most of the food supply must be filtered away by the large windward reefs. The filtering efficiency of a reef can be remarkably high, as was shown by Glynn (1973; 1973a). Over a Porites reef flat he found an efficiency of 91 percent for diatoms and of 60 percent for zooplankton. The filtering effect of the unusually wide reef flats involved here must be considerable. Moreover, a rather large part of the Saba Bank lies too deep. Indeed, constructional coral growth may occur even down to depths of 40 m (Glynn, 1973a: p. 281) but Adey and Burke (1976: p. 108) observed that, in the eastern Caribbean, major bank-barrier systems did not develop on shelves more than 20-25 m deep.

In the lagoon there are large areas of calcareous bedrock, so sedimentation is not a limiting factor for the settlement of corals. In fact many corals have settled there and the number of species is not significantly lower than on the reef. The colonies just remain small in size and number. As in most other atoll lagoons, constructional coral growth is restricted to small patch reefs.

If the windward reefs have developed during the last 5 000 years (Goreau, 1969: p. 324), as all modern reefs have, the amount of reef accumulation has been considerable in this area. The maximum height of these reefs is 6-12 m above the level of the lagoon, while Milliman (1973: p. 41) reports a reef accumulation of less than 1 m in Florida and less than 7 m in Jamaica. Of course, it must not be excluded that the reefs grew on pre-existing rims, although the presence of such rims cannot easily be explained.

The presence of the front reefs is very difficult to explain. Of course, the presence of a reef along the edge of a terrace is quite normal, but in this case the greater part of the terrace lies at the same depth as the lagoon floor, which means that in most areas the front reef and the large reef must have developed simultaneously. In some areas the base of the front reef lies at a considerably lower level than the base of the large reef and, here, reef formation could start earlier, i.e., before the surface of the island was flooded. Even if parts of these reefs had more than 5 000 years available, their great height (even up to 20 m) is quite remarkable.

The innermost of the north reefs lies at the same level as the windward reefs. The relatively meagre coral growth in this area is undoubtedly due to its unfavourable leeward position.

All other reefs lie at a lower level. Their bases lie at a depth of more than 40 m and their tops never reach to a water depth of less than 30 m. In my opinion these reefs started growing when the greater part of the Saba Bank was still an island, i.e., when the seawater was still 20-30 m below the present level. Consequently they originated as leeward fringing reefs. In this situation a considerable reef accumulation in the area can easily be imagined, in the first place because of the shallow water and in the second place because a leeward position off an island often facilitates rather than retards coral growth. The only problem is it is generally accepted that the level of the seawater rose rather rapidly towards the end of the last glacial period and, if this is true, only a comparatively short time has been available for the development of these reefs.

I find it difficult to relate the terrace and reef base levels with those of platforms in other parts of the Caribbean. According to Goreau (1969: p. 324) drowned reef platforms are often found at -60, -40 and -25 m levels, while Milliman (1973: p. 41) states that 18 and 35 m terraces are present on many islands. Terrace levels on the Saba Bank are too variable to allow sensible comparisons. Moreover some terraces slope gradually over considerable distances.

9. THE ATOLL QUESTION

Vaughan (1919: p. 304) has already suggested that the Saba Bank (and the Rosalind and Pedro Banks) could be compared with atolls by stating "these banks are scientifically of great importance, for, except that the coral growth is not so luxuriant, they essentially duplicate the great atolls in the Pacific". Nevertheless, Bryan (1953) did not mention the Saba Bank in his list of 27 possible Caribbean atolls. Milliman (1973: p.20) estimated that there are only about ten atolls in the Caribbean and did not include the Saba Bank in his list either. Indeed, until now, the Saba Bank could hardly be called an atoll with certainty because of lack of information. We can now put forward on a firmer basis the question as to whether or not the Saba Bank must be considered an atoll.

On the map presented here (Fig. 2) the Saba Bank shows all the characteristics of a typical atoll; but we have to admit that this map is somewhat misleading because the depth factor is not included. It is still necessary, therefore, to discuss the atoll question in some detail.

Atolls do not have a particular shape and, in fact, the classical circular atoll is comparatively rare (Wiens, 1962). In many atolls the peripheral reefs carry one or more islands, but this is certainly not always the case. In some cases there is a single peripheral reef completely encircling the lagoon, but in most atolls there are one or more channels connecting the lagoon with the open sea. In most Caribbean atolls the lack of leeward peripheral reefs even results in relatively open lagoons (Milliman, 1973: p. 24). Although volcanic activities nearly always have played an important role in the geologic history of atolls, one of the most important characteristics of atolls is the almost complete absence of outside terrigenous influences.

With the preceding rules in mind and comparing the Saba Bank with other Caribbean atolls (described most excellently by Stoddart, 1962, 1971, 1973) we may conclude that it must be considered an atoll. However, we have reason to believe that the leeward reefs, including the southwest reef and the northwest reef, are not now growing significantly and that they should be considered drowned reefs. Consequently they do not belong to the present atoll system. For the same reason, submerged atolls, on which modern coral growth appears to be insignificant, must be considered fossil atolls. Such drowned atolls are particularly common in the Indian Ocean (Stoddart, 1973).

It must be concluded, therefore, that only the eastern and largest part of the Saba Bank can be called a living atoll with an open lagoon, while the western part is a bank with drowned fringing reefs.

Whether the western part is included or not, the Saba Bank ranks among the largest atolls in the world, its surface area being of the same order as those of the Suvadiva Atoll in the Maldives (2 240 km^2; see Stoddart, 1971: p. 7) and Kwajelein in the Marshalls (1 683 km^2; see Wiens, 1962: p. 28). The size of its living reefs is also remarkable. According to Wiens, (1962: p. 113) the width of atoll reefs is usually not more than 500 m, although in the Moluccas, reef widths of 2-2.5 km do occur.

A better knowledge of the Saba Bank would be important, not only for comparative atoll studies of the Caribbean region, but undoubtedly also for a better understanding of the Caribbean reefs in general. Therefore, I hope that our preliminary observations, which raised rather than answered questions, will be considered a challenge for future, more detailed, research in the area.

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STUDY OF THE MACRO-FAUNA OF THE TROPICAL WESTERN ATLANTIC

by

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CONTENTS

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2. DESCRIPTION OF THE CRUISES
3. COLLECTIONS
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Abstract

From 1964 to 1975 the writers collaborated in a large-scale investigation of the kinds, numbers and distribution of the macro-fauna of the tropical Atlantic Ocean from West Africa to the Caribbean and the Gulf of Panama in the eastern tropical Pacific. Support was obtained from the National Geographic Society and the National Science Foundation and the work was conducted mainly on board the University of Miami's research vessels GERDA and JOHN ELLIOTT PILLSBURY. Work in 1964 and 1965 was undertaken mostly in West African waters and the Straits of Florida but, since 1966, studies were conducted in tropical Atlantic waters from Surinam to the Bahamas. R/V GERDA occupied 1 348 stations, mostly in the Straits of Florida, but her operations extended to Arrowsmith Bank and the southern Bahamas. R/V PILLSBURY occupied 1 132 stations, ceasing operations in 1971 when she was retired from the fleet. From 1972 through 1975 cruises were made aboard the R/V JAMES M. GILLISS and consisted of 134 stations. The PILLSBURY and GILLISS stations were located every 15-30 miles apart around the circumference of the Caribbean and northeastern South America from the intertidal to a depth of 8 650 m in the Puerto Rico Trench, where 31 stations were made, mostly with 12.5 m otter trawls. The collections obtained were sorted and are maintained at the University of Miami with all data entered into a computer system.

Including its inaugural cruise in June 1972, the R/V COLUMBUS ISELIN has made 10 cruises and 442 stations associated with macrobiological studies, mostly in conjunction with a quantitative study of the benthic fish fauna of the Tongue of the Ocean and Exuma Sound, Bahamas.

More than 30 collaborators have been, or are, working on the invertebrate collections. More than 125 papers have been published on the results, a major contributoon to our knowledge of the marine fauna of the tropical western Atlantic.

Resumen

Entre 1964 y 1975, los autores colaboraron en una investigación a gran escala con el fin de determinar la variedad, cantidad y distribución de la macrofauna del océano Atlántico tropical, desde el Africa occidental hasta el Caribe y el golfo de Panamá, en el Pacífico tropical oriental. Se obtuvo ayuda para el proyecto de la National Geographic Society y la National Science Foundation y los trabajos se realizaron principalmente a bordo de los buques de investigación GERDA y JOHN ELLIOTT PILLSBURY, de la Universidad de Miami. En 1964 y 1965 se trabajó principalmente en aguas del Africa occidental y en el estrecho de La Florida, pero a partir de 1966 se realizaron estudios en aguas del Atlántico tropical, desde Surinam hasta las Bahamas. En total, el GERDA realizó trabajos en 1 348 puntos, sobre todo en el estrecho de La Florida, pero también en el banco Arrowsmith y en el sur de las Bahamas. El PILLSBURY realizó trabajos en 1 132 puntos, interrumpiendo las operaciones en 1971, año en que se retiró de la flota. Desde 1972 hasta 1975 se hicieron viajes con el buque de investigación JAMES M. GILLISS, que recaló en 134 puntos. Los puntos de trabajo del PILLSBURY y el GILLISS estaban situados a 15 - 30 millas de distancia unos de otros, alrededor de la circunferencia del Caribe y el nordeste de América del Sur, desde la zona de mareas hasta una profundidad de 8 650 metros en la fosa de Puerto Rico, donde se trabajó en 31 puntos, principalmente con redes de arrastre de 12,5 metros. Las muestras obtenidas se clasificaron y se conservan en la Universidad de Miami, donde todos los datos se han incorporado en el sistema de computadoras.

Incluso su primero crucero en junio de 1972, el B/I COLUMBUS ISELIN ha realizado 10 cruceros, visitando 442 puntos relacionados con estudios macrobiológicos, por la mayor parte en el curso de un estudio cuantitativo de los peces del fondo en el área de Tongue of the Ocean y Exuma Sound, en las Bahamas.

Más de 30 colaboradores han trabajado o están trabajando sobre esos datos, y con los resultados de los mismos se han publicado ya más de 125 trabajos, que representan una importante contribución a los conocimientos actuales sobre la fauna marina del Atlántico tropical occidental.

1. INTRODUCTION

In January 1964 Drs. Gilbert L. Voss and Frederick M. Bayer received funds from the National Geographic Society to initiate a broad, long-term study of the fauna of the shelf, slope and deep sea of the tropical Atlantic. Both were invertebrate specialists so they solicited the interest and cooperation of Dr. Robins to handle the vertebrate side of the programme. One of the many graduate students at the laboratory who participated in the early cruises was Dr. Jon C. Staiger. He continues his interest, eventually taking over much of the ship operations and was Chief Scientist on many of the later cruises. The cost of the operation of the ships came from the National Science Foundation, which also provided the support for numerous individual research programmes carried out in conjunction with the ship operations.

Specifically we proposed to study the geographical and vertical distribution of the bathypelagic and benthic faunas, their composition, origin, and ecological requirements. We proposed to study these faunas from the continental shelf down the slope to the deep basins and the bottom of the Puerto Rico Trench. Although our major studies were to be ocean-wide, we also proposed a more detailed study of the Straits of Florida because of its unusual configuration and the fact that its bottom sediments and hydrography were well known (Voss, 1973).

Most broad-scale, ocean system studies have been done from the standpoint of physical and geological oceanography. It has seldom been possible to put together a continuous, broad programme in biology of the nature we proposed. We considered however that the time was propitious because of the availability of many new and improved types of collecting equipment such as benthic trawls, midwater high speed trawls, new and improved trawling cables, modern winches and better ships. All these were conducive to better survey work and, with the use of computer systems, the results could better assimilate hydrographic and geological data along with the biological input.

We chose the tropical Atlantic as our area of research by reason of our previous preoccupation with the region and the interests of our staff of biologists. Study of the total tropical Atlantic was considered essential to an understanding of the effects of the major tropical ocean currents on the transport of larvae from Africa to the Americas, or its reverse, and the desire to evaluate this supposed system. Similarly, studies of the eastern tropical Pacific were early envisioned by reason of the peculiar geological history of the Isthmus of Panama and the long duration of connexion between the Caribbean Sea and the Pacific Ocean.

Four ships were used. The smallest was the GERDA, 23 m long, a converted yacht built in Denmark on the lines of a North Sea trawler. She was used in the Straits of Florida, on Arrowsmith Bank and in the southern Bahamas, although on earlier occasions she had made several long cruises as far as Curaçao. Gear used included 3 m otter trawls, 1.8 m Isaacs-Kidd trawls and small dredges.

The workhorse of the fleet was the JOHN ELLIOTT PILLSBURY. She was 53.6 m long, a converted former U.S. Army FS and fully equipped for trawling. She had a large Western Gear winch which held 12 700 m of 14.3 mm oceanographic wire rope; this length permitted us to trawl in the deepest areas in the ocean. When the PILLSBURY was retired in 1971, she was replaced by the 63.7 m AGOR the JAMES M. GILLISS. The winch from the PILLSBURY was installed on the GILLISS and the latter now has the deepest trawling capability of any ship in the U.S. Atlantic fleet of oceanographic vessels. She is rigged to trawl from the stern, a distinct advantage in certain weather conditions.

Finally, in the same year, the GERDA was replaced by a larger vessel, the COLUMBUS ISELIN, of 53.3 m but without the depth capability of the GILLISS. She carries 9 120 m of 12.5 mm wire.

All involved in the programme were adamant that as wide a variety of gear as possible should be used in order to get the best sampling of the variety of bottom life. While we attempted to make uniform tows with each piece of gear, the nature of the bottom in the Caribbean often prevented quantitative sampling. We believe the variety of gear used has permitted us to obtain a fairly representative picture of the various faunas. These sampling devices included box dredges; oyster dredges; grabs; 3,7.6, 12.2 and 12.4 m otter trawls and semiballoon trawls; 3 m Blake trawls, surface plankton nets; 1.8 and 3 m Isaacs-Kidd trawls and a 3 m Tucker opening and closing net. Extensive night lighting was done at every opportunity, with very satisfying results (Voss, 1966).

At the same time, the value of selecting certain key, or representative, areas to study quantitatively with standardized gear was recognized as the region became better known, and a programme was started in 1972, supported later by the National Science Foundation, in the deep Bahama basins. This programme is described later.

2. DESCRIPTION OF THE CRUISES

The first two cruises of 1964 and 1965 were in West Africa, from Liberia to the Congo Rise and the islands of Fernando Póo and Annobon (Voss, 1966a). On these two islands we were struck by the great similarity of the intertidal and shallow water insular faunas with those of the Caribbean. Both the benthic tows and those from midwaters were much richer than any made later in the Caribbean region, certainly attributable to the fact that this is an area of general upwelling and high nutrient levels.

Our cruise in 1966 was in the southwestern Caribbean, covering the area from off Cartagena, through the Gulf of Urabá and along the coast westward to Escudo de Veragua, Panama. The bottom along much of this region is coral and we lost many nets, especially in the western region (Voss, 1967).

In 1967 we took the PILLSBURY into the Pacific and undertook a survey of the fauna of the Gulf of Panama from Punta Mala, on the west, to Cabo Caracoles, on the east (Voss, 1968). This region was very rich in numbers and variety of species and compared favourably with similar stations in the Gulf of Guinea. In fact, where our standard shelf tow in the Caribbean was of 30 minutes duration, the tows in the Gulf of Panama had to be reduced to 10 minutes in order to be able to get the nets back aboard.

In 1968 two cruises were made. The first was for two weeks to the northwestern Caribbean and Arrowsmith Bank in cooperation with the Mexican Government (Staiger, 1969). The second was of a months duration from Paramaribo, Surinam, to Cartagena (Staiger, 1969a). This cruise had originally been planned for Brazilian waters, but permission to enter these waters was revoked at the last minute and the cruise was rerouted. Instead, we entered Paramaribo and then worked northward into the Caribbean and westward to Cartagena. As of this date we have been unable to work in Brazilian waters and an integral part of our programme is missing. If programmes like ours are to succeed, international cooperation must be assured. Such cooperation exists between the various scientists, but unfortunately it does not always occur between governments.

The following year (1969) two more cruises were made with the PILLSBURY. The first was for two weeks to the Puerto Rico Trench where we first experienced trawling below 6 000 m. Despite abominable weather, in which green seas broke over the ship, we made several successful tows on the bottom of the Trench and proved to ourselves that, with a few changes of gear, a survey of the Trench was indeed practicable.

The second cruise of that year was a full month. It originated in Port of Spain, Trinidad, and terminated in Miami (Staiger, 1971). The ship worked the full extent of the Windward and Leeward Islands, including several shore stations at Martinique and Guadeloupe. Three tows were also made in the Puerto Rico Trench as the ship passed over it.

The first cruise in 1970 was back to the Trench. This time the weather was beautiful. Our first tows were again made with the Blake trawl, but we changed to the 12.4 m trawl and found that it was remarkably easy to use, even in those great depths; it has since been our standard net below 6 000 m.

The second cruise, again of a months duration, departed from Miami. Work began in the southern Bahamas and offshore from the west end of Haiti and into the Bay of Gonave. From there the ship proceeded to the south coast of Jamaica and around the west end to Montego Bay, where part of the scientific crew was changed. The ship then headed for Pedro Bank, working its entire length. A run was made to Cabo Beata in the Dominican Republic. The south coast of Hispaniola was trawled to the east end from whence we ran to the St. Croix Basin, made several tows and terminated the cruise in San Juan (Staiger and Voss, 1971).

In 1971 we returned with the PILLSBURY to Escudo de Veragua and worked northward along the coast to Cabo Grácias a Diós, with a brief stop at Providencia where we did reef collecting. This cruise completed our circumnavigation of the Caribbean; the few intervening areas were worked in shorter cruises with the GERDA.

In the summer of 1971 we again took the PILLSBURY to the Trench and, after completing our work there, did some trawling along the southeast side of Hispaniola and in the St. Croix Basin. This cruise terminated in St. Thomas and was the last voyage of the JOHN ELLIOTT PILLSBURY, which was then retired for the new ship, the JAMES M. GILLISS.

Our first cruise with the GILLIS was to the Gulf of Panama in order to finish up the work we had commenced in 1967. We worked from Cabo Caracoles to Cabo Corrientes and made a series of deep-sea hauls beyond the edge of the slope.

During the same summer we again took this ship on a months cruise, working exclusively in the deep basins of the Caribbean Sea, the Yucatan Basin south of Cuba, the Colombian Basin and the Venezuela Basin. After a short stay in Curaçao, we continued trawling in the Venezuelan Basin toward the Aves Ridge. Several bottom tows on the west slope of the Aves Ridge yielded volcanic ash, volcanic glass and pumice - presumably from the 1902 eruption of Mt. Pelée on Martinique.

With the termination of funds from the National Geographic Society, the survey work came to an end. However, special funds were obtained in 1974 for the final phase, which comprised a series of stations in two long transects of about 1 600 km, one on each side of the mid-Atlantic Ridge.

The Puerto Rico Trench continued to occupy our interest and, in 1975, the GILLISS spent three weeks trawling the Trench, the St. Croix Basin and the Oriente and Bartlett Deeps. We also took advantage of the opportunity to make a series of stations south of Cuba in the Yucatan Basin from opposite Cienfuegos to the Isle of Pines.

During all these years, until the GERDA was laid up, work was also underway in the Straits of Florida from the Yucatan Channel to Fort Pierce, Florida. Here we laid out a grid, dividing the Straits into 1.6 km squares, and we have attempted to make at least one bottom and one midwater trawl in each square; 1 348 stations have been occupied in this general area. To date we have completed 3 056 stations ranging in depth from the intertidal to 8 650 m (Fig. 1).

3. COLLECTIONS

In past expeditions, where large numbers of stations and material have been handled, numerous specimens have arrived back in the laboratory in such poor condition that they were unfit for study. On our cruises, as work progressed around the clock, the scientific party was divided into three watches of four persons each, with at least one fish specialist on each watch; the others were divided as nearly as possible to give broad coverage of the invertebrates. The contents of the trawl were worked over as quickly as possible, but with

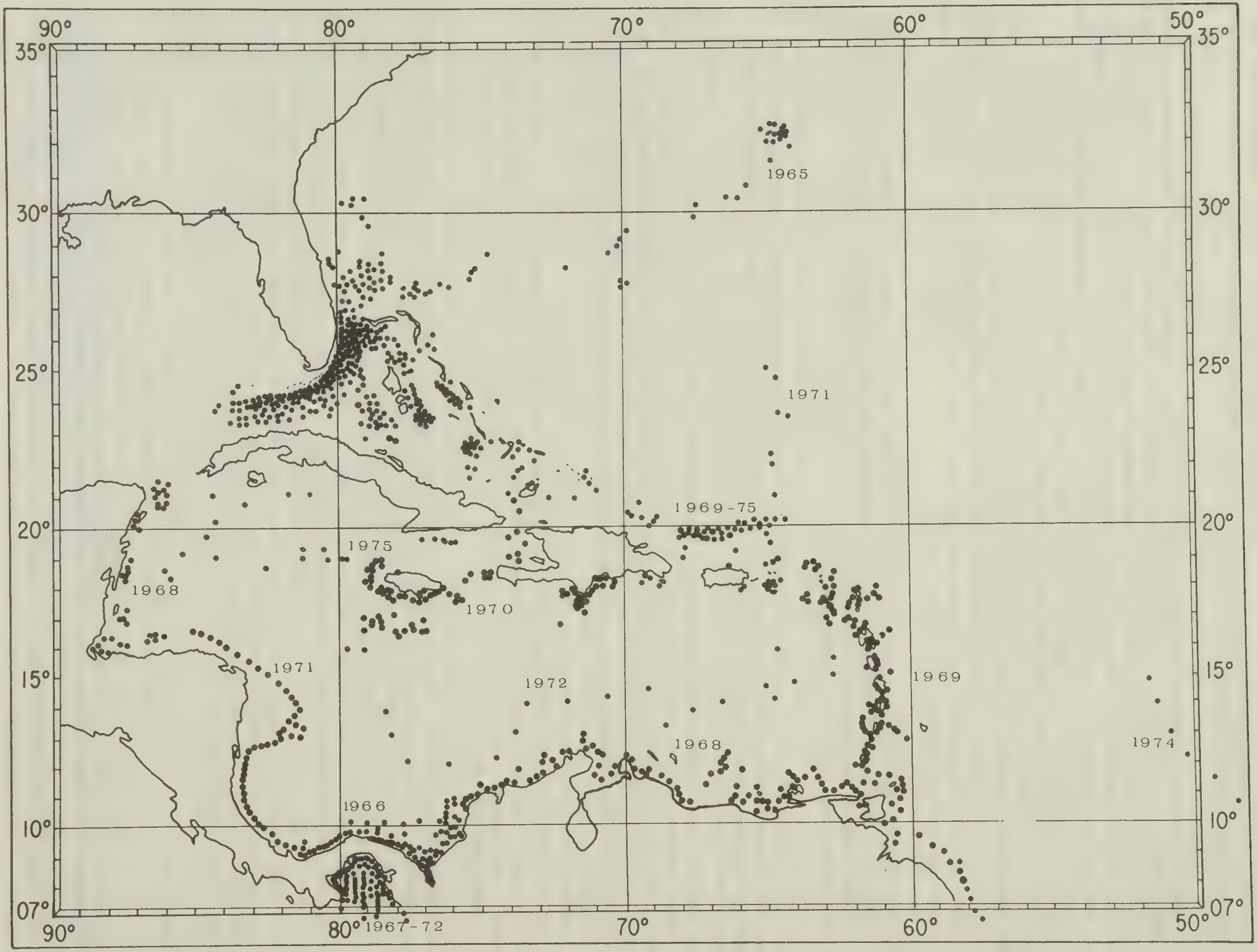
90°
80°
70°
60°
50°
35°
30°
25°
20°
15°
10°
07°
1965
1971
1969-75
1975
1968
1970
1971
1972
1969
1968
1974
1966
1967-72

Fig. 1 Stations in the western Central Atlantic occupied during University of Miami macro-fauna survey cruises

great care. All specimens of uncommon species were sorted out and retained; representative samples of the common and numerous species were retained and a note entered into the scientific log as to the numbers discarded. The specimens were preserved carefully in their appropriate medium; some were frozen for anatomical or biochemical study and all were noted in the log.

In preserving soft, deep-sea specimens, immediate preservation is an absolute necessity. Hence, soft-bodied invertebrates were either plunged immediately into buckets of near-freezing water and then taken to the lab for fixation, or were dropped immediately into 70 percent alcohol. Fish were fixed in 10 percent freshwater formalin. In all cases this must be done within a couple of minutes from the dumping of the cod end of the net, or the specimens disintegrate in the hot sun, in some cases visibly deteriorating into jellylike masses in a matter of one or two minutes. These soft-bodied animals also required several changes of alcohol within the first 48 hours of capture.

All the collections were returned to Miami and there sorted by our staff of sorters. All specimens were counted and the numbers of each group entered on station data sheets. We have now sorted all the stations from our regular programme and the number of macro-invertebrates well exceeds one million specimens.

These collections are stored at the museum and are sent out to specialists either as requested, or as we can find specialists who will agree to work them up. At present more than 30 collaborators in this country and abroad are working on various groups of invertebrates, but many groups are still in the stacks; either interested specialists have not been contacted, or there are no specialists in this country or abroad for the particular group.

As originated by the invertebrate specialists, the primary interest of the programme was to determine zoogeographical patterns and community structure; it was of prime importance therefore that absolute control be maintained over the collections and the results of their study. Thus no invertebrate specimens are loaned for study unless the specialist agrees in writing to forward to us identifications of the species, number and sex of each and size of the largest and smallest specimens in each lot. Each paper published using our invertebrates is given a number in the series resulting from our work. In this way we have been able to maintain a complete record of all identifications and a full list of all literature resulting from the invertebrate side of the studies. These data are entered into our data retrieval system and, eventually, when the other results have been published, will be used for final analysis of distribution and community or association complexes. The only combined fish and invertebrate data which have been thus analysed so far are those resulting from our studies on the two sides of the Isthmus of Panama carried out in cooperation with the studies on the practicality of an interoceanic, sea level canal, and supported by the Canal Commission. More will be said about this later.

4. RESULTS

In a programme as large as ours, where the number of invertebrates alone exceeds a million specimens, and the data from over 3 000 stations need to be worked up, it will be many years before even the majority of the data are completed. The magnitude of the task may be better understood if one recalls that the CHALLENGER, on her four-year voyage, made only 240 successful dredge and trawl stations.

Even so, we can now point to a number of interesting, but preliminary, results. I should preface this by stating that, at the present time, over 125 papers have been published on the results of our programme and numerous others are in press. A list of all of the published papers is given in the Appendix. Some of these papers are small and consist of descriptions of new species. Others are monographic in nature. The monograph of the brachiopods, by Dr. Cooper of the Smithsonian Institution, is as important to modern brachiopod research as was the CHALLENGER monograph when it was published. It will be published this summer.

One of the features that struck us in 1966 in the southwestern Caribbean was the extremely large amount of organic debris encountered on the slope in depths from about 300 to 1 000 m in the area from Colón to off the Golfo de Morrosquillo. This consisted of the remains of terrestrial plants such as mangroves, bananas, coconut fibres, water lettuce, and other types of material washed into the sea from the steep shore.

While this great accumulation of organic material should have led to an increase in benthic life, it appears that it was too great for the system to accommodate, and the reverse was true. Where the debris was heavy there was less life of all types, although we found only very slight indications of hydrogen sulfide. Inshore, on the shelf, the amount of bottom debris was normal so that either it must be transported off very quickly or it does not become waterlogged until some days in the sea, by which time it is farther offshore. In the cruise in 1972, at a distance of about 160 km offshore from this area and in depths of 3 700 m, heavy accumulations of terrestrial vegetable material were encountered.

Surprisingly our only other area of heavy plant debris accumulation has been in the Puerto Rico Trench. In the western end, at a depth of around 8 500 m, the plant debris was in such quantities that the bottom was anoxic. When the trawl came to the surface on the last three tows made in this area, the stench of hydrogen sulfide was so great it was difficult to work with the material, and almost no animals were found. Even the red clay, usually heavy and sticky in the trench, was brownish and soupy. Working farther eastward this accumulation of plant debris, perhaps dumped into the trench by currents from the Mona Passage, diminished greatly and the animal life increased correspondingly. To our knowledge, our findings on this subject are the first in trench literature.

It is too early to say very much about the geographical distribution of life in the Caribbean. Our impression is, however, that, as might be suspected, there are considerable differences in species and numbers between the insular regions, with small shelf areas and hard bottom, and the wide extent of shelf along the mainland, with intermittent sand, mud, and coral reefs. We are confirmed thus in our belief of an insular versus continental fauna in the West Indies. (This was discussed in detail for fish by Robins, 1971.) Some may object that this is purely ecological, to which we will agree. What stronger factors affect zoogeography in the sea?

On the continental side, it appears that there may be a break between the northern South American fauna and the Central American fauna opposite the mouth of the Gulf of Uraba. There is a striking change there but, until further analysis, it may be that this is more apparent in local trawling than in reality.

Studies of the ichthyofauna of shore and shelf areas in the Caribbean region have demonstrated a definite distinction between insular and continental species assemblages. The continental fish fauna can be divided into northern and southern components. The northern tropical continental fish fauna occurs from Cape Canaveral, Florida, through the Gulf of Mexico to Yucatan and, in somewhat reduced form, around Cuba, Hispaniola, and Jamaica. The southern counterpart occurs from Brazil to the northern coast of Venezuela. Along the coast of Colombia and Central America the northern and southern components occur together in estuarine areas and over muddy substrates offshore from river mouths. The insular fish fauna occurs from the Windward Islands to the Bahamas and around Aruba, Bonaire, Curaçao and Las Roques. It is also found associated with clear water and reef areas along the coasts of Colombia, Central America, Cuba, Hispaniola and Jamaica. In addition to the obvious differences between the species compositions of the continental and insular fish faunas, there is also a difference in dominance-diversity. The continental ichthyofauna is less diverse than the insular fauna, and usually dominated by relatively few species. The insular fauna is more speciose and the number of individuals more equally apportioned.

Our studies do not indicate a strong break in the Antilles. Unfortunately we have not had the opportunity to conduct trawling in Cuban waters, where an extensive shelf should

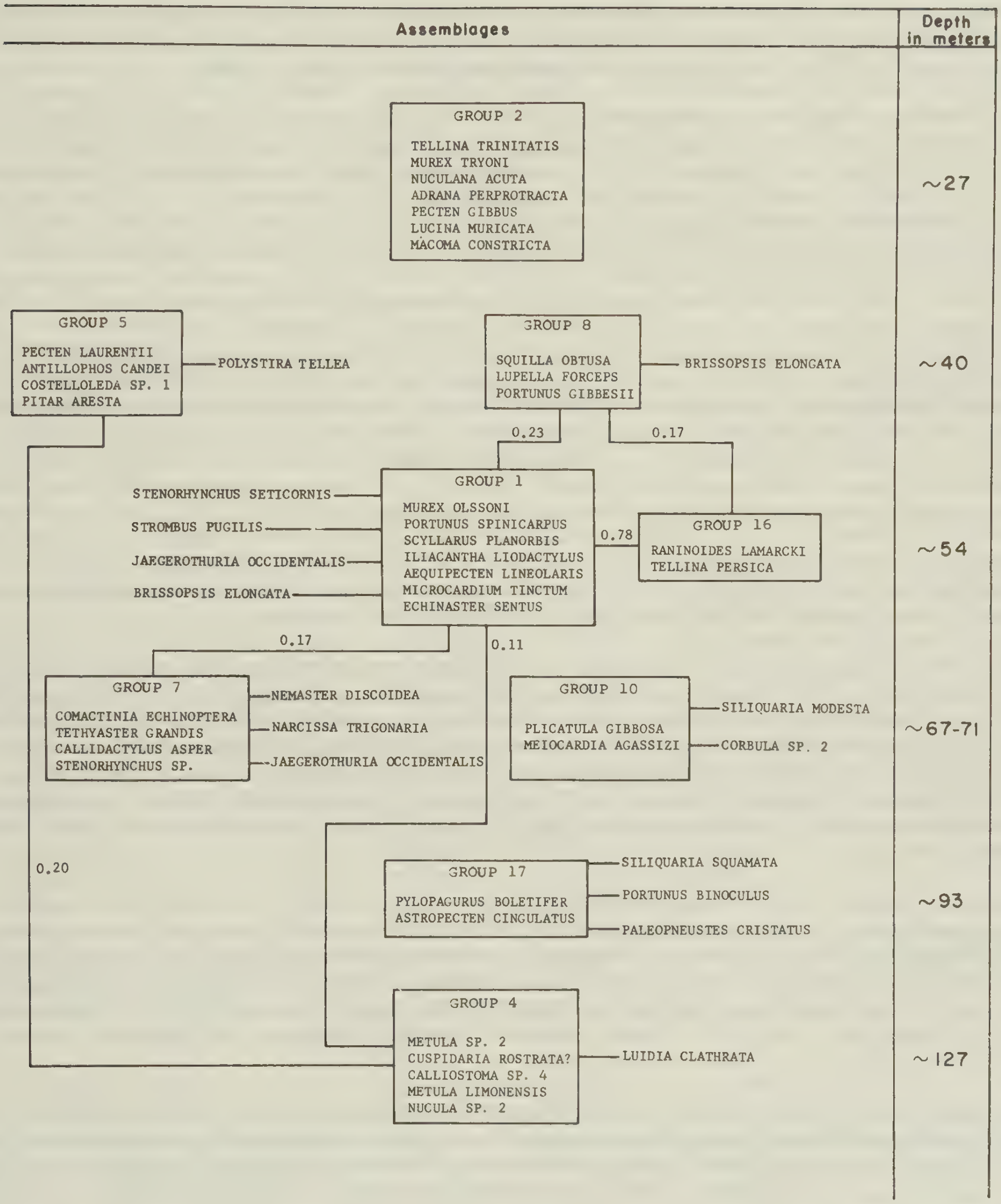
Assemblages
Depth in meters
GROUP 2
TELLINA TRINITATIS
MUREX TRYONI
NUCULANA ACUTA
ADRANA PERPROTRACTA
PECTEN GIBBUS
LUCINA MURICATA
MACOMA CONSTRICTA
~27
GROUP 5
PECTEN LAURENTII
ANTILLOPHOS CANDEI
COSTELLOLEDA SP. 1
PITAR ARESTA
POLYSTIRA TELLEA
GROUP 8
SQUILLA OBTUSA
LUPELLA FORCEPS
PORTUNUS GIBBESII
BRISSOPSIS ELONGATA
~40
0.23
0.17
GROUP 1
MUREX OLSSONI
PORTUNUS SPINICARPUS
SCYLLARUS PLANORBIS
ILIACANTHA LIODACTYLUS
AEQUIPECTEN LINEOLARIS
MICROCARDIUM TINCTUM
ECHINASTER SENTUS
STENORHYNCHUS SETICORNIS
STROMBUS PUGILIS
JAEGEROTHURIA OCCIDENTALIS
BRISSOPSIS ELONGATA
0.78
GROUP 16
RANINOIDES LAMARCKI
TELLINA PERSICA
~54
0.17
0.11
GROUP 7
COMACTINIA ECHINOPTERA
TETHYASTER GRANDIS
CALLIDACTYLUS ASPER
STENORHYNCHUS SP.
NEMASTER DISCOIDEA
NARCISSA TRIGONARIA
JAEGEROTHURIA OCCIDENTALIS
GROUP 10
PLICATULA GIBBOSA
MEIOCARDIA AGASSIZI
SILIQUARIA MODESTA
CORBULA SP. 2
~67-71
0.20
GROUP 17
PYLOPAGURUS BOLETIFER
ASTROPECTEN CINGULATUS
SILIQUARIA SQUAMATA
PORTUNUS BINOCULUS
PALEOPNEUSTES CRISTATUS
~93
GROUP 4
METULA SP. 2
CUSPIDARIA ROSTRATA?
CALLIOSTOMA SP. 4
METULA LIMONENSIS
NUCULA SP. 2
LUIDIA CLATHRATA
~127

Fig. 2 Invertebrate assemblages of the Caribbean continental shelf

unite the insular faunas of the Antillean Arc with the continental faunas from across the Yucatan Channel. Voss and Voss (1960) have already indicated that the fauna of the Florida Keys is composed of a mixture of Continental and Antillean species and no doubt this is also the case with the island of Cuba with its high mountains, heavy rainfall, and muddy embayments which favour the continental species (Robins, 1971, 1972).

As indicated earlier, the only region where our studies have been subjected to final analysis is the area from Cartagena to Escudo de Veragua and the corresponding area in the Pacific (Bayer, Voss and Robins, 1970). With special funds from the Canal Commission through the Batelle Memorial Foundation, we were able to have nearly 1 700 species of invertebrates and fishes identified from there and the Gulf of Panama for study of their relationship and community structure. This report has still not been issued in final form.

All the 1 700 species belonging to the alcyonarians, molluscs,crustaceans, echinoderms and fish were subjected to recurrent groups analysis for uniting in assemblages or associations (Fig. 2). In each of these we determined the dominant species and attempted to determine the numbers of analogous or twin species on the two sides of the Isthmus. An interesting feature of our analysis was that certain communities were nearly identical on each side of the Isthmus and, in those particular associations, the dominant species were the same or similar. Furthermore, our analysis showed that about 30 to 50 percent of all the species in most groups were the same or similar on the two sides; convincing proof, if such were needed, for the very late closure of the Isthmus.

Comparison of the catch data from both sides of the Isthmus indicated that the productivity of the Gulf of Panama is 3 to 5 times greater than that of the southwestern Caribbean, a reflection of the upwelling in the Gulf of Panama.

One of the characteristic features of the shelf fauna of the Caribbean is the high percentage of sponges of numerous species. Although few commercial species were taken, others filled the nets and, in two places, the north end of the Golfo de Morrosquillo and off and around Cabo Beata, Hispaniola, two widely separated regions, a soft, crumbly sponge filled the nets and caused intense, but luckily of short duration, burns from either a toxin or spicules. Despite this sponge, the Golfo de Morrosquillo showed large numbers of commercial shrimp and a large scallop, Pecten laurentii, in quantities sufficient to support a fishery.

Another mollusc which occurred in sufficient quantities to warrant investigation for exploitation was Arca zebra on Pedro Bank. This so filled the nets they were often too heavy to swing aboard and the net, surging in the seas beside the ship, sounded as if it were filled with crockery. These are large bivalves with a great deal of solid meat. The shells must be in great quantities: some are loose, others are attached to small pieces of rock or alcyonarians, while most were fastened to each other in long strings of half a dozen or so.

Trawling in two areas was greatly impeded by the presence of coral outdrops. Normally one would not set a trawl in such areas but, as we were interested in what occurred and where, sampling was necessary. Along the coast of Panama from Colón to Escudo de Veragua, the bottom is smooth and clean except for scattered small outcrops of corals, unpredictable in their occurrence and frequency. A single jolt of the trawl wire usually indicated that the net had been badly torn or left on the bottom. By the time we reached our last station off Escudo de Veragua, we had not a single entire net on board.

The other difficult trawling region was in the neighbourhood of Cabo Beata and the Isla de Alta Vela, Hispaniola. Only the closest collaboration between the man at the precision depth recorder, the man at the winch, and the bridge made it possible to sample successfully this very rich area. The results were well worth the hazards.

In considering the wealth of bottom life in the shelf waters of the West Indies, the dominant character would seem to be the presence of corals, turtle grass, sponges, and that seemingly ubiquitous crab, Lupella forceps.

In the deeper waters of the slope and basins, we took some of our most interesting animals. During the course of our investigations we made trawling transects across the floor of each of the Caribbean basins, sometimes several transects. The fauna of these basins is rather rich. From some we have taken astoundingly large brotulid fish and others. Our invertebrates have ranged from ahermatypic corals, *Umbellula* and weird glass sponges, to large lobsters of several genera, and scaled squid. It is interesting that the large isopod, *Bathynomus giganteus*, is not commonly found in the lower Caribbean, although common in the gorge west of Quito Sueño Bank. They are voracious animals and feed ravenously upon animals in the net while the tow is in progress.

The number of smaller ahermatypic corals such as *Deltocyathus* must be enormous in these basins. Almost every tow brings up an ooze of their dead skeletons. Other ahermatypic corals are also very numerous; it is always surprising that these very delicate skeletons, with fragile septa, come up in nearly perfect condition.

Study of the distribution of the fish of the Macruridae and Brotulidae (both dominant families of deep-sea fishes) yielded interesting results. On the slope we find several assemblages differentiated by depth and type of substrate over which they occur. The deepest slope assemblage, which occurs on smooth muddy bottom, ranges out onto the floor of the deep basins, but in a considerably reduced form.

The work in the Trench and the deeps has been very rewarding. We have now made over 30 successful tows in the Puerto Rico Trench and can report that the diversity of invertebrate life is very high. Almost every species taken there was a new depth record for the Atlantic, including the deepest capture of any fish so far recorded, a species of *Bassogigas* taken from a depth of 8 350 m. Most of the material has not been published upon as yet, but numerous new species were taken. Among the surprising finds were two not yet explained. One was the occurrence of both nodules and laminated sheets of the iron pyrite, marcasite, apparently not before reported from deep-sea locations. It is supposed to be laid down under reducing conditions, but the water just above the bottom is well oxygenated. This action must take place in the clays, The other was finding the remains of the carcass of a large squid in about 8 000 m. While Anton Bruun hypothesized that carcasses of surface animals might fall to the sea floor and there form focal points for animal life, none has ever before been reported from a trench or an ocean basin. Apparently most remains are consumed quickly by a host of bottom feeders, such as isopods, but this squid was still fresh, probably because of the very cold water of the trench floor.

In our last cruise in 1975 we also turned up some interesting depth records. From the Bartlett Deep we took from 7 280 m numbers of a small white chiton and a finned octopod of the genus *Grimpoteuthis*. The chitons exceeded their known depth range by several hundreds of metres, while the cephalopods previously were known from no deeper than 5 600 m, a record also set by us from the Nares Abyssal Plain.

On our last cruise we encountered some new hazards to deep trawling. While we are used to bringing up all sorts of garbage from the floor of the Trench, we were quite unprepared on this cruise to foul the nets twice on sunken naval gunnery targets and target barges in the St. Croix Basin and to pick up in the nets, at widely divergent stations, four anti-submarine sonobuoys with attached insulated hydrophone wire.

As the material is worked up, areas of special interest for more detailed comparative studies are beginning to become evident; these would not have been located without a survey type study first. It is also clear that, without such a programme as we are conducting, the general patterns of zoogeography cannot be truly delineated. The fact that we have collected many new fish species and an average of 25 to 30 percent new species in every invertebrate group studied from our material only indicates the paucity of our knowledge of the Caribbean fauna. As the major groups of animals are published upon, it is our intention to prepare charts showing the distributions, both geographical and vertical, of the West Indian fauna. Later community analysis will aid our interpretation of our faunas.

We believe the results we are getting are sufficient proof that surveys are still a serious lack in our attempts to interpret the biology of the oceans. Nowhere is this lack more evident than along our own coastline in eastern North America. Unfortunately the study of the macro-fauna has dropped far behind the study of the plankton, mainly because of the cost and the greater time consumed in making the stations, but also due to the unfortunate belief in many circles that surveys are outdated and all monies should be placed on measures of productivity, diversity, and on environmental models. Unless this attitude is changed, or overcome, the needed surveys of shelf and slope waters of Brazil and more detailed transects in the areas already sampled by our programme will have to be funded by, or at least initiated by, the countries concerned. We stand ready to cooperate and conduct joint programmes where proper government funding and support by scientific nationals are present. These efforts can be combined with training programmes dealing at all levels from technicians to M.S. and Ph.D. candidates. We have no doubt that the number of stations occupied for macro-faunal studies is less than one percent of those made for plankton.

A detailed study was made of benthic fish distribution in the Straits of Florida, the area of heaviest sampling effort and density. Analysis of the fish from 280 stations between 200 and 1 700 m depth demonstrated the existence of six distinct patterns of distribution and seven species assemblages which conform to these distributions. Combinations of substrate preference and depth range appear to be the factors delineating the seven assemblages.

In recent years Dr. Robins has led a programme to study, on a quantitative basis, the benthic fish of the Tongue of the Ocean and Exuma Sound, two deep, sill-less basins that cut into the Bahamian shelf. The 12.4 m semi-balloon trawl is set at predetermined stations, hauled for a prescribed length of time, and retrieved, Each station is repeated from cruise to cruise and at least one, usually three, stations are repeated within a cruise. All fish are retained, weighed, their length measured, and sex and stage of maturity determined. Samples of all invertebrates are retained. 'Catchability' of the rather weak-swimming fishes at these depths is equal for all species so comparison of actual numbers is possible for all except the rare species. It has already been demonstrated that, although the fish at these depths in these basins are living in a seasonally unchanging environment, at least certain species in each major group spawn seasonally, and often at opposite seasons. The importance of surface isotherms and the physiological adaptations of such early stages of fish as are passed above the thermocline are of the greatest importance in determining latitudinal limits of these deep-dwelling benthic fish. In addition to the basic goals of this programme, this detailed study will permit us to choose certain stations from our tropical Atlantic survey and compare them quantitatively against our Tongue of the Ocean "metre stick". Wherever comparable gear was operated without disruption for sufficient time to obtain a critical sample size, the results can be statistically adjusted and compared. This we hope to do for benthic fish in the 1 550 to 3 000 m range.

We cannot subject each area of the ocean to such intensive study but, by selection of key areas for such study, together with continuation and completion of the vital surveys, extrapolation can be made and the complex fauna of the tropical Atlantic will be better understood. We wish to take this opportunity to thank the National Geographic Society which supported this programme for ten years and provided salaries, travel funds, nets, and the sorting facilities for handling the collections.

5. ACKNOWLEDGEMENTS

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7. APPENDIX

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A REVIEW OF BENTHIC COMMUNITY RESEARCH IN THE CARIBBEAN AND ITS IMPORTANCE TO COASTAL MANAGEMENT

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Abstract

Recent advances in benthic community research have not been widely applied in the Caribbean area to problems of coastal management. However, there is increasing awareness of the usefulness of benthic research in the detection and monitoring of coastal changes and a number of these studies have been conducted in parts of the Caribbean since CICAR-I in 1968. One such study performed by this author has been an investigation of the soft bottom communities in Kingston Harbour, Jamaica and the effect of organic pollution on them.

Since 1968 when the communities were first examined, considerable changes have occurred as a result of decreasing oxygen levels. Of four original communities, two have been completely destroyed resulting in the spread of a large abiotic zone. One highly stressed community has become dominated by the polychaete Capitella capitata, while a previously healthy community has begun to show rapid deterioration. In every case, there has been a trend of decreasing species diversity, increasing dominance by a few species and a shift in population concentrations to nearer the open sea.

Two polychaete species (Spiochaetopterus oculatus and Capitella capitata) have shown high resistance to heavy pollution while three other species (Poecilochaetus sp., Magelona sp. and Scolaricia sp.) which now dominate the healthier community, appear to withstand moderate pollution. Several other species also show various levels of pollution tolerance.

An understanding of the pattern of changes in the Kingston Harbour communities and of the sensitivity of various species to different levels of pollution can be useful tools in the detection and prediction of pollution effects elsewhere.

Resumen

Los progresos que se han registrado recientemente en las investigaciones sobre comunidades bentónicas no han encontrado amplia aplicación a los problemas de la ordenación de las zonas costeras del área del Caribe. Por otro lado, cada día hay mayor conciencia de la utilidad de las investigaciones bentónicas para detectar y vigilar los cambios que se producen en las zonas costeras, y desde que comenzaron las ICCRA-I, en 1968, se han realizado varias investigaciones de ese tipo en algunas partes del Caribe. Una de ellas, realizada por el autor del presente trabajo, ha consistido en un estudio de las comunidades de los fondos fangosos de la bahía de Kingston, en Jamaica, y de los efectos que tiene en ellos la contaminación orgánica.

Desde 1968, año en que se examinaron por primera vez esas comunidades, se han producido cambios considerables debido a la disminución del nivel de oxígeno. De las cuatro comunidades que existían originalmente, dos han desaparecido completamente, lo que ha dado lugar a una amplia zona abiótica. En una comunidad muy afectada por la contaminación se ha producido un predominio del poliqueto Capitella capitata, mientras otra comunidad antes sana ha empezado a dar signos de rápido deterioramiento. En todos los casos se ha manifestado una tendencia a la disminución del número de especies, un mayor predominio de algunas especies y un desplazamiento de las concentraciones de población hacia alta mar.

Dos especies de poliquetos (Spiochaetopterus oculatus y Capitella capitata) han mostrado ser muy resistentes a la contaminación intensa, mientras otras tres especies (Poecilochaetus sp., Magelona sp. y Scolaricia sp.) que actualmente predominan en la comunidad más sana, parecen poder resistir una contaminación moderada. También otras especies han mostrado distintos niveles de tolerancia a la contaminación.

Conocer los cambios experimentados por las comunidades de la bahía de Kingston y la sensibilidad de las distintas especies a diversas concentraciones de contaminación puede ser útil para detectar y predecir los efectos de la contaminación en otras zonas.

1. INTRODUCTION

Any attempt at coastal resource management must involve the prevention or abatement of pollution. In order to do this, it is necessary to be able to detect signs of pollution and to monitor it, to have some predictive insight into its possible effects and to understand the causes.

The usefulness of marine benthic organisms in detecting and monitoring pollution has long been recognized and many workers have studied the benthos as a means of measuring the degree of pollution in an area as indicated by its changes. Two recent review papers by Reish (1972) and Pérès and Bellan (1972) stressed the practical application of such work but, whereas the former emphasized the single species method, favouring in particular the indicator organism concept, the latter stressed a population, or community, approach to pollution monitoring. However, whichever approach is taken, and there is normally scope for both, there is no doubt that the validity of the methods has been well established and their convenience, due to the fairly simple and standard techniques employed, proven. Benthic ecologists throughout the world have been gathering an increasing body of information on the benthos and the effects of pollution on it and, recently, there have been rapid advances both in the scope and the level of understanding of the subject. For these reasons, use of the benthos for monitoring pollution in the Caribbean should be most attractive.

2. BENTHIC RESEARCH IN THE CARIBBEAN

Most of the work done on the benthos in the Caribbean has been directed toward the ecology of single species rather than of communities, few only having been related to pollution problems. Hence, despite the variety of benthic communities in the Caribbean and the uniqueness of many, our knowledge and understanding of them is still rudimentary. For example, it is surprising that there have been very few surveys undertaken to describe what communities exist in coastal waters, much less to describe how they function. Some examples are the works of Rodriguez (1959, 1963) in Venezuela; Newell, Imbrie, Purdy and Thurber (1959) in the Bahamas; Lewis (1965) in Barbados; Roberts (1971) in Grand Cayman and now Swain and Hull (this symposium), also in Grand Cayman. These studies provided a general inventory of the coastal communities in these places and yet, by and large, they have covered relatively small areas only. Much more of this kind of work is necessary, therefore, to include more of our coastal environments, otherwise how can we make a series attempt at managing our coastal resources unless we know what these resources are?

Of Caribbean coastal benthic communities, I wish to mention five I think important and to discuss the work done on four of these. The five are the sand beach community, the turtle grass community, the sandy reef lagoon community, the mud bottom community and the coral reef community (see Stoddart, this symposium, for a discussion of coral reef communities).

The sand beach community of the Caribbean is, probably, better understood than the others, due to the work of Dahl (1953), Rodriguez (1959), Wade (1967) and Dexter (1972, 1974). All the workers have shown that this community bears close similarity to sand beach communities throughout the world and, therefore, is not unique to the area. Primarily it is a physically stressed community with, generally, few species dominating in large numbers of individuals. Dexter (1974) applied the Shannon-Wiener and Fager indices of diversity and evenness to nine communities she studied in Costa Rica and Colombia; the results provided good mathematical support to the earlier descriptions of low diversity and evenness for this community.

The marine phanerogams _Thalassia testudinum_ (turtle grass), _Halophila baillonis_, _Syringodium filiforme_ and _Diplanthera wrightii_ are abundant subtidally in lagoons and on reef flats throughout the Caribbean and form the distinct benthic environment commonly referred to as turtle grass or seagrass beds. Despite the high primary and secondary productivity of these seagrass beds and the diverse fauna associated with them, relatively little work has been done on their ecology. Furthermore, most of this work has been conducted in sub-tropical waters in Florida although, within the past five years or so, there has been increasing activity in the Caribbean.

The Caribbean work falls into two main categories. First is the growth of Thalassia and its relation to grazing activity, especially by echinoids and fish (Greenway, 1974, 1974a; Ogden, 1974; Vincente, 1975). Second is the distribution and abundance of the benthic fauna associated with the seagrass (Jackson, 1972, 1973; Rivera and Vincente, 1975; Keller, personal communication). So far, only Jackson (op. cit.) has attempted any form of community analysis for the zoobenthos of the Caribbean seagrass beds although O'Gower and Wacasey (1967) have done similar work in Florida. These studies have particular importance because they have sought to relate community structure to environmental variables caused both by biotic and physical factors. Hence, in addition to recording the species found in the seagrass beds, the communities have been described with respect to their diversity, evenness, abundance and stability under different conditions. Unfortunately, however, the work in Florida was limited to a small area in two localities, while Jackson's studies in Jamaica dealt almost entirely with the molluscan fauna. There is, consequently, much scope for further work along these lines and it is surprising, therefore, that more similar work is not being undertaken in the Caribbean, where seagrass beds are so abundant and accessible.

The paucity of studies on the production, energetics and community structure of seagrass beds in the Caribbean has left us mostly ignorant as to how this system functions. This situation needs to be remedied soon since, clearly, the beds play an important role in the maintenance of a rich coastal environment. Furthermore, if we wish to use this benthic community for detecting and monitoring subtle changes in the coastal environment, then our knowledge of how it responds to various environmental variables will have to be improved greatly. To me, this appears urgent since the seagrass communities occupy a large proportion of the Caribbean coastal environment, especially where man-made effects are most likely to occur due to waste discharges and engineering works.

The third benthic community of interest is that of the predominantly sandy lagoon behind fringing reefs. The bulk of the bottom sediments here are formed from foraminifera and Halimeda segments; gorgonians, molluscs and echinoderms occur in large numbers. Isolated coral heads can occur in deeper parts, while dead coral and coral rubble form substrates for sessile organisms throughout the lagoon.

Kinzie (1973) and Preston and Preston (1975) have studied the gorgonian fauna of the sand and rubble and also patch reef areas in Jamaica and Puerto Rico. Kinzie has shown that the main factor limiting the distribution of gorgonians in the lagoon is the availability of a firm substratum, while Preston and Preston have found that the gorgonians interpret their patch reef environment as stable in spite of a siltation stress. Thus, while Kinzie found a Shannon diversity value for the gorgonian fauna in the lagoon zone of 2.20, Preston and Preston found a higher level of 3.43 on the patch reefs.

It is clear from these studies that the gorgonian fauna in lagoon areas is more sensitive to the stability of the substratum than to stresses imposed by the nature of the water above the colonies. The same might also be true for other sessile organisms of the lagoon area, but this needs to be examined. With a better understanding of the entire epifaunal community of the lagoon area, it is possible that this community could be used as a sensitive indicator of lagoonal instability brought about by coastal works, e.g., channelling and harbour construction.

The final benthic community to be considered is the mainly infaunal one of the soft sands and muds occurring in many kinds of locations. Despite great increase in interest in these communities throughout the world, there has still been little work done on them in the Caribbean, this being largely confined to Venezuela, Puerto Rico and Jamaica.

In Venezuela, Lopez and Okuda (1968) and Lopez (1971) investigated the distribution of the macrobenthic fauna with respect to the physico-chemical characteristics of the sediments in the Grand Lagoon of Obispo and in the Cariaco Trench. However, although these studies related population densities of the entire fauna and the major taxa (annelids, arthropods, sipunculids and molluscs) to shifting conditions, no attempt was made to analyse the structure of the community in terms of number and kinds of species, their distribution within the community and their biological interactions.

In Puerto Rico, Phelps (1966) studied the benthos in Añasco Bay, primarily to determine how stable elements were partitioned within two communities in connexion with radio-ecological studies conducted for the U.S. Atomic Energy Commission. Although this work was so aimed, it has provided useful information on species composition of the communities and their feeding types. It is a pity that, although this work has provided such good preliminary information, it does not seem to have been pursued toward a greater understanding of the nature of these communities.

Seiglie (1968, 1971, 1973) studied the foraminiferal assemblages in the mud bottoms of several bays in Puerto Rico and provided useful information on the composition of these assemblages as well as on the relationships of some of them to pollution. Although he pointed out the usefulness of certain species as indicator organisms, I have no evidence that they have actually been used for monitoring pollution in Puerto Rico or elsewhere.

Work in Jamaica has been more oriented toward describing the nature of the soft bottom communities and their relationship to environmental variables than have been the others in the Caribbean. For example, Aller and Dodge (1974) produced a most interesting paper on the infaunal community of the reef lagoon at Discovery Bay and related diversity and trophic structure to gradients in bottom stability brought about by sediment size, biogenic reworking and water circulation. To my knowledge, this is the first timethe community of this area, often regarded as barren, has been described; it is also the first serious attempt to examine animal sediment relationships in such a predominantly carbonate environment. The scope and possibilities for future such work are tremendous.

Reeson (1971) studied the benthic fauna in a hypersaline coastal lagoon near Port Royal, on the south coast of Jamaica and related the species composition, diversity and density of the community to the greatly fluctuating conditions which exist from the dry to wet seasons. His work provided much useful information on the kind of infaunal community which might develop in a greatly, but naturally, physically stressed environment in tropical waters. I have not seen this kind of work duplicated in the Caribbean or anywhere else in the tropics.

My own work, which began in Kingston Harbour in 1968, was aimed originally at describing the nature of tropical soft bottom communities and relating them to the stable environmental conditions which exist only in tropical waters (Wade, 1972a). However, no sooner had we obtained preliminary results than it became abundantly clear that most of the harbour communities were being affected by physiological stress due to low oxygen levels and/or periodic salinity fluctuations (Wade, 1972). Only the community in the outer part of the harbour near the open sea appeared to be truly healthy and typical of what one might expect in a stable tropical environment. As our work continued, we saw deterioration taking place in all the communities such as could not have been predicted after our first survey (Wade, Antonio and Mahon, 1972). We pursued our investigations further with two main aims in view: (a) To identify the nature of the changes which were taking place so rapidly among the harbour communities; (b) to elucidate the specific causes of these changes in terms of the immediate and long-term factors.

These expressed aims demanded that we examine closely the nature of the communities with which we were dealing and that we begin to look critically at thoseenvironmental factors which could possibly affect the way these communities were being structured. At the outset all the preliminary evidence seemed to implicate increasing organic pollution as a major factor in the determination of the communities. Thus, without expressly stating it, we soon found that we were very much involved in monitoring pollution in the harbour through the investigation of the benthic communities.

The report of our studies is in preparation (Wade, 1976) and I shall only be able to outline the major findings here. In so doing, I hope to show how a study of the benthos in Kingston Harbour has been used to reveal both gross and subtle changes taking place in the harbour régime and how a simply designed and executed benthic monitoring programme can provide information which can only be obtained otherwise by elaborate and extensive water quality and sedimentary studies.

3. THE BENTHOS AND POLLUTION IN KINGSTON HARBOUR

3.1 The Study Area

Kingston Harbour is a semi-enclosed bay situated on the south coast of Jamaica (Fig. 1). It is bounded on the north, east and west by the mainland coast and on the south by a narrow spit of land, the Palisadoes; entrance to the open sea is by a channel at the southwest corner. Total area is 51 km^2. There are three main regions, the Inner Harbour, the Outer Harbour and Hunts Bay. The first two are mainly deep basins (9.5–18.3 m deep) while Hunts Bay is shallow and has been cut off from the rest of the harbour by a solid-fill causeway. There are also extensive sand shoals in the Inner and Outer Harbours.

Fresh water enters the harbour at Hunts Bay by two rivers and a drainage scheme as well as along the northern shore by way of several intermittent gully courses. Primary treated sewage effluent (approximately 8 mgd) and various untreated industrial wastes are also discharged into the Inner Harbour and Hunts Bay, especially from the industrial complex extending from Newport East to Newport West.

Tides have a mean range of only 23.5 cm and currents are mainly wind-generated and of low velocity, never usually exceeding 30 cm/sec. However, prevailing winds from the southeast can reach up to 40 km/h, the result of which is much vertical mixing of the water column. Except in Hunts Bay, salinity is normally between 35 and 36 parts per thousand.

Surface water is normally saturated with oxygen (Fig. 2). However, except for the Outer Harbour, all other parts have oxygen deficiency at the bottom and there is a definite decline as one moves up the harbour and into deeper water. The worst conditions, therefore, occur in the bottom water at the extreme eastern end of the harbour. Since 1971, these bottom oxygen conditions have been deteriorating; the greatest deterioration has been in Hunts Bay and the Outer Harbour.

Sediments consist of clays and silts in the deep basins and Hunts Bay, and sands and gravels on the shoals. Seagrass beds cover extensive areas of the sand flats.

3.2 The Original Communities

In 1968 over 100 stations on the sand and mud bottoms were sampled using a 1/10 m^2 van Veen grab. Analysis of the samples revealed the presence of five distinct level bottom communities - one in the sand and four in the mud (Fig. 3). The sand community was moderately diverse and was dominated by the lancelet *Branchiostoma caribaeum*. Over forty species were recognized, the majority of which were suspension feeders.

Within the Inner Harbour, two mud communities were recognized. The first, consisting of only eleven species, occurred in the eastern section and was dominated by the tubiculous polychaete *Spiochaetopterus oculatus*, which accounted for 96.4 percent of the total number of individuals. The second community, found in the greater part of the Inner Harbour, was dominated by the related polychaete *Chaetopterus variopedatus*. This community consisted of 35 species and *C. variopedatus* accounted for 47.0 percent of all individuals.

The third mud community occurred in Hunts Bay and was dominated by the opheliid polychaete *Armandia* species and the snapping shrimp *Alpheus* species, along with *Capitella capitata*. There were 21 species, but none accounted for more than 24.5 percent of all individuals.

The fourth mud community was found in the Outer Harbour and was marked by its extremely high diversity (150 species). No single species dominated numerically and, together, the two most common species comprised only 16.4 percent of all individuals.

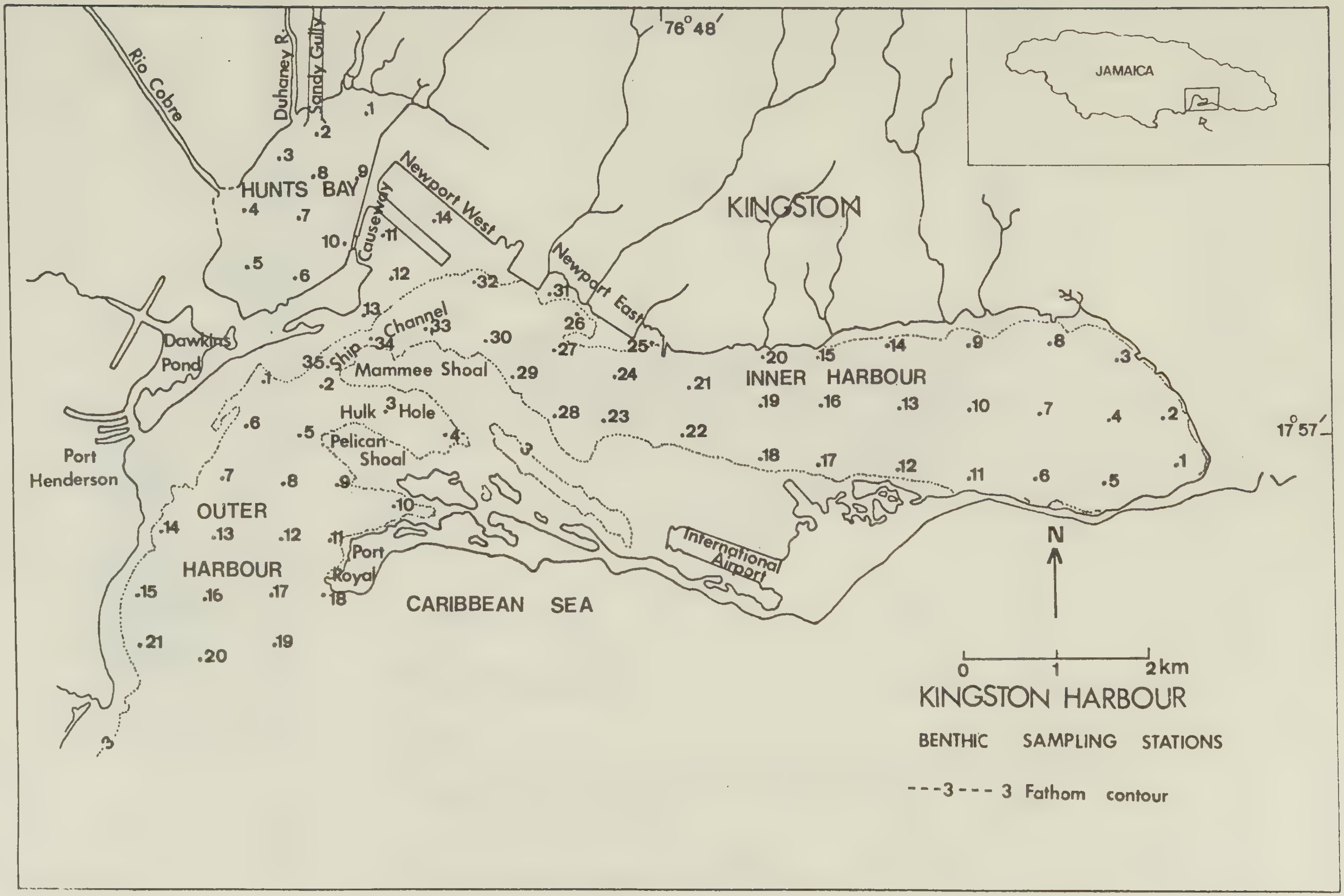

JAMAICA
KINGSTON
76°48′
17°57′
Rio Cobre
Duhaney R.
Sandy Gully
HUNTS BAY
Causeway
Newport West
Newport East
Dawkins Pond
Port Henderson
Ship Channel
Mammee Shoal
Hulk 3 Hole
Pelican Shoal
INNER HARBOUR
OUTER HARBOUR
Port Royal
International Airport
CARIBBEAN SEA
N
0
1
2km
KINGSTON HARBOUR
BENTHIC SAMPLING STATIONS
---3--- 3 Fathom contour

Fig.1 Map of Kingston Harbour, showing the major features and the benthic sampling stations

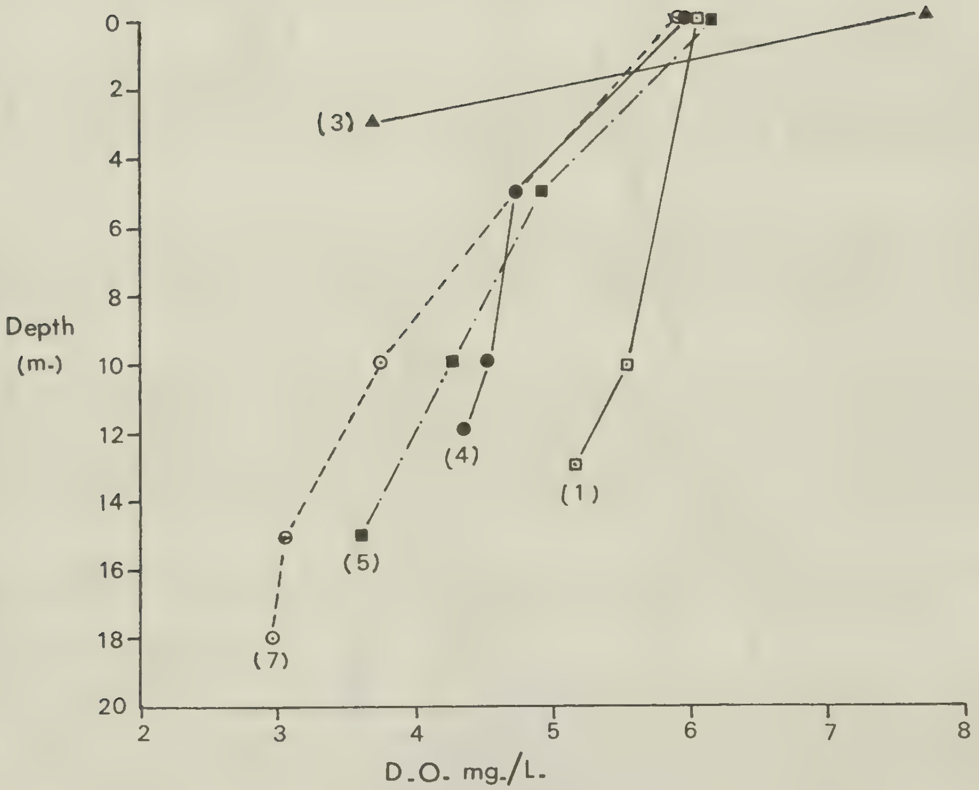
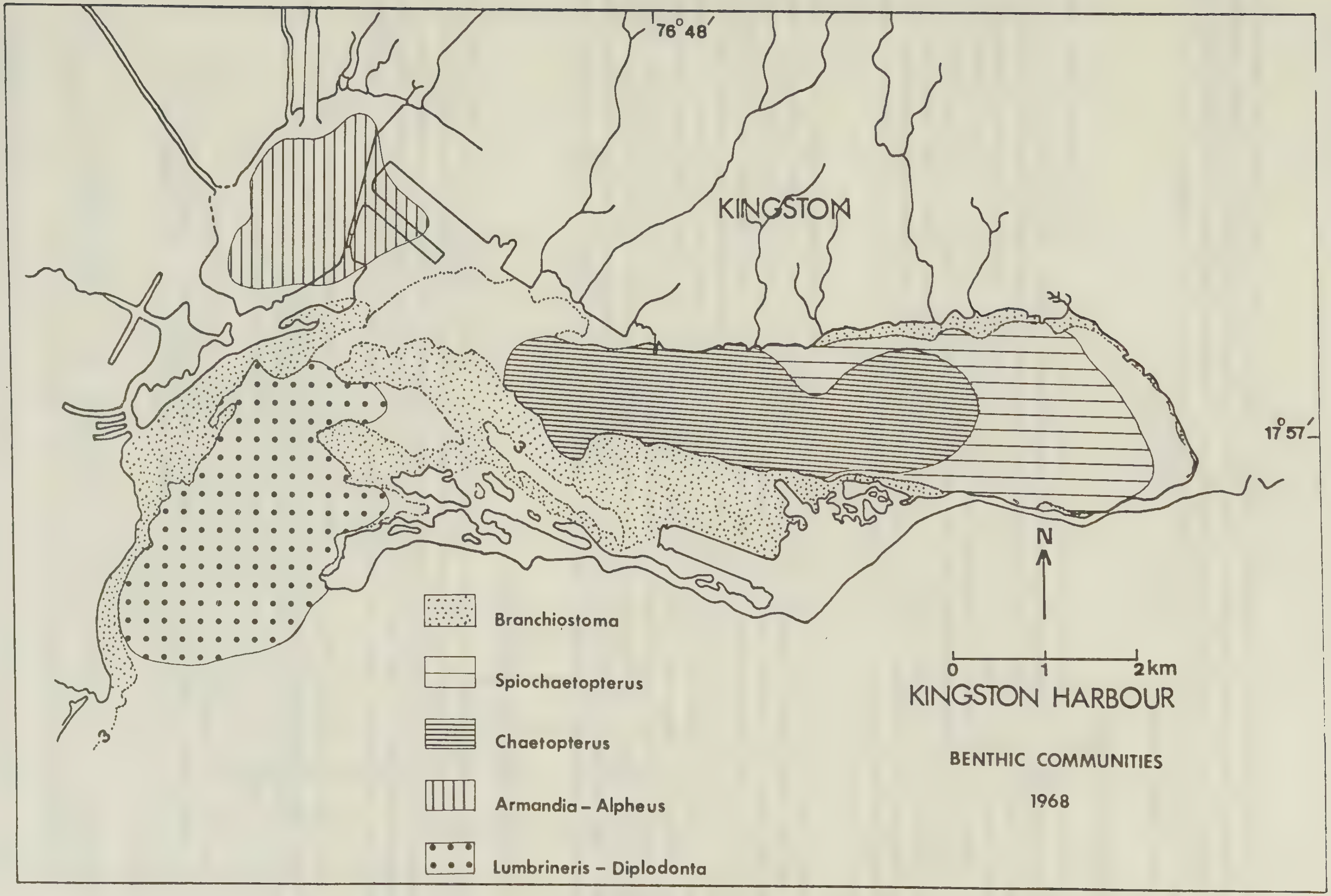


Fig. 2 The average dissolved oxygen profiles for 5 monitoring stations in Kingston Harbour for 1973-1975:

(1) Outer Harbour
(3) Hunts Bay
(4) Inner Harbour (West)
(5) Inner Harbour (Central)
(7) Inner Harbour (East)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17°57′
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2km
KINGSTON HARBOUR
BENTHIC COMMUNITIES
1968
Branchiostoma
Spiochaetopterus
Chaetopterus
Armandia – Alpheus
Lumbrineris – Diplodonta

Fig. 3 Distribution of the five level bottom communities in Kingston Harbour in 1968

This pattern of communities revealed a steep increase in diversity from the eastern end of the Inner Harbour and Hunts Bay out to the Outer Harbour and indicated a rapid improvement of the environment over a relatively short distance. Evidence indicated that this was due primarily to a gradient in bottom oxygen conditions brought about by organic pollution originating from the Inner Harbour.

3.3 The Pollution Pattern

From 1968 to 1974 four surveys of the mud communities of the entire harbour were carried out and the harbour zoned according to the number of species taken per 1/10 m^2 grab sample at each station. These zones were: (a) A zone of no species, representing maximum pollution (very polluted zone); (b) A zone of 1-5 species, representing heavy pollution (polluted zone); (c) A zone of 6-10 species representing mild pollution (semi-healthy zone) and (d) A zone of more than 10 species representing no pollution (healthy zone). Although the zones were demarcated according to the number of species taken, other criteria such as density of individuals, degree of dominance and presence of indicator species were also employed to interpret the pollution pattern. Results of the surveys for the first and last years are shown in Figs. 4 and 5.

They show that between 1968 and 1974 a zone of maximum pollution appeared in the eastern end of the harbour and spread rapidly westward to occupy most of the Inner Harbour. Similarly, in 1972, another zone of maximum pollution appeared in the Newport East area and, by 1974, this had spread in both directions along the northern shore of the harbour and out into the shipping area. By 1974 this new zone had also become contiguous with that spreading from the eastern end. In 1971 a zone of heavy pollution developed in Hunts Bay following its enclosure by the solid-fill causeway. By 1974 this zone also extended out from Hunts Bay and into the shipping area. Due to this massive spread of pollution from these three areas, only a small section of the Inner Harbour could be zoned as semi-healthy or only mildly polluted by 1974 and this was in the area nearest the Outer Harbour. Throughout the surveys the Outer Harbour community remained healthy. However, as we shall see later, it also suffered several changes.

3.4 Effect of Pollution on Populations

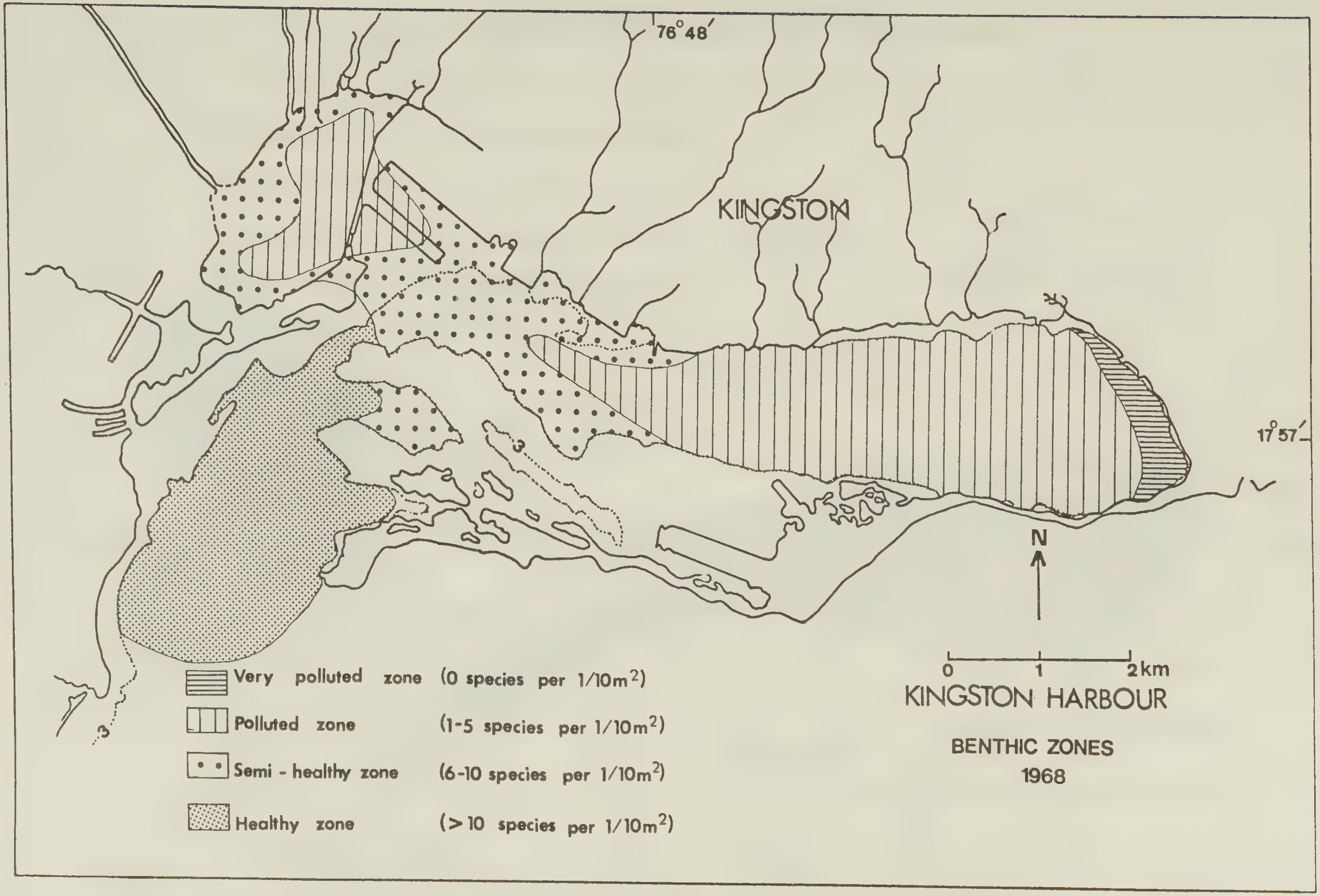
As pollution spread, the distribution and density of all the species in the Inner Harbour and Hunts Bay, as well as most of those in the Outer Harbour, changed. Basically, nearly all showed a common trend of retreating toward the Outer Harbour and nearer the open sea. However, there was much variation in the rate at which different species retreated and how their densities responded to different levels of pollution. The species fall into three categories:

(1) Those which reached their highest densities in the heavy polluted zone, e.g., *Spiochaetopterus oculatus* and *Capitella capitata*. As maximum pollution spread, these species were the last to disappear. However, as they retreated to the Outer Harbour, their densities decreased (Fig. 6).

(2) Those which reached their highest densities in the semi-healthy or mildly polluted zone, e.g., *Poecilochaetus* sp. and *Magelona* cf. *berkeleyi*. As they retreated, both their distribution and density in the Outer Harbour increased (Fig. 7).

(3) Those which occurred only in the healthy zone, e.g., *Lumbrineris* sp., *Diplodonta punctata*. As pollution advanced, they showed a steady decrease in distribution and density in the Outer Harbour (Fig. 8).

The varying responses of these species to the deteriorating environment represent different levels of tolerance to organic pollution; hence, they can be used as indicator organisms for these environments throughout the Caribbean.


76°48′
KINGSTON
17°57′
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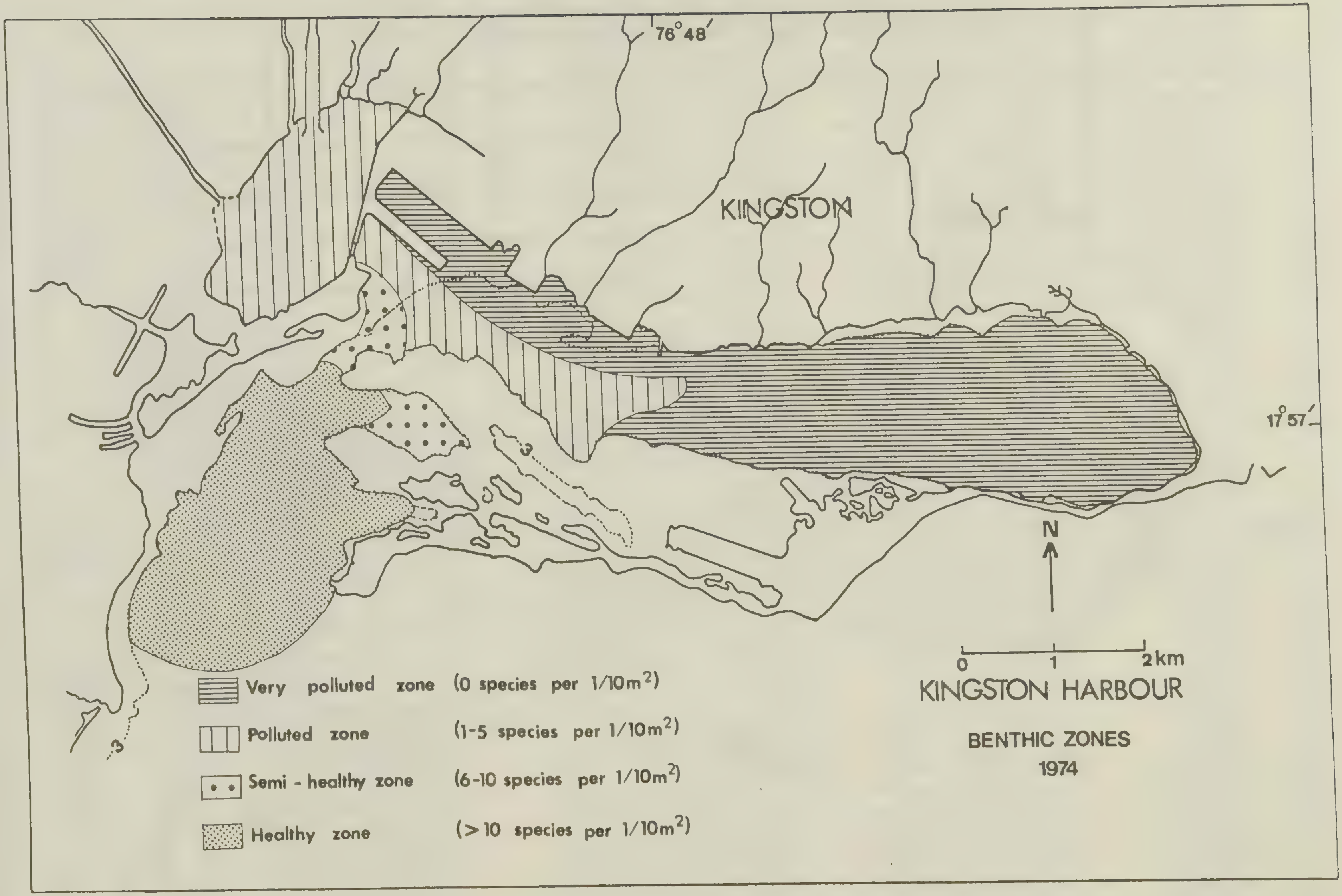
0 1 2km
KINGSTON HARBOUR
BENTHIC ZONES
1968
Very polluted zone (0 species per 1/10m²)
Polluted zone (1-5 species per 1/10m²)
Semi - healthy zone (6-10 species per 1/10m²)
Healthy zone (>10 species per 1/10m²)

Fig. 4 Distribution of the benthic zones in Kingston Harbour in 1968, showing the levels of pollution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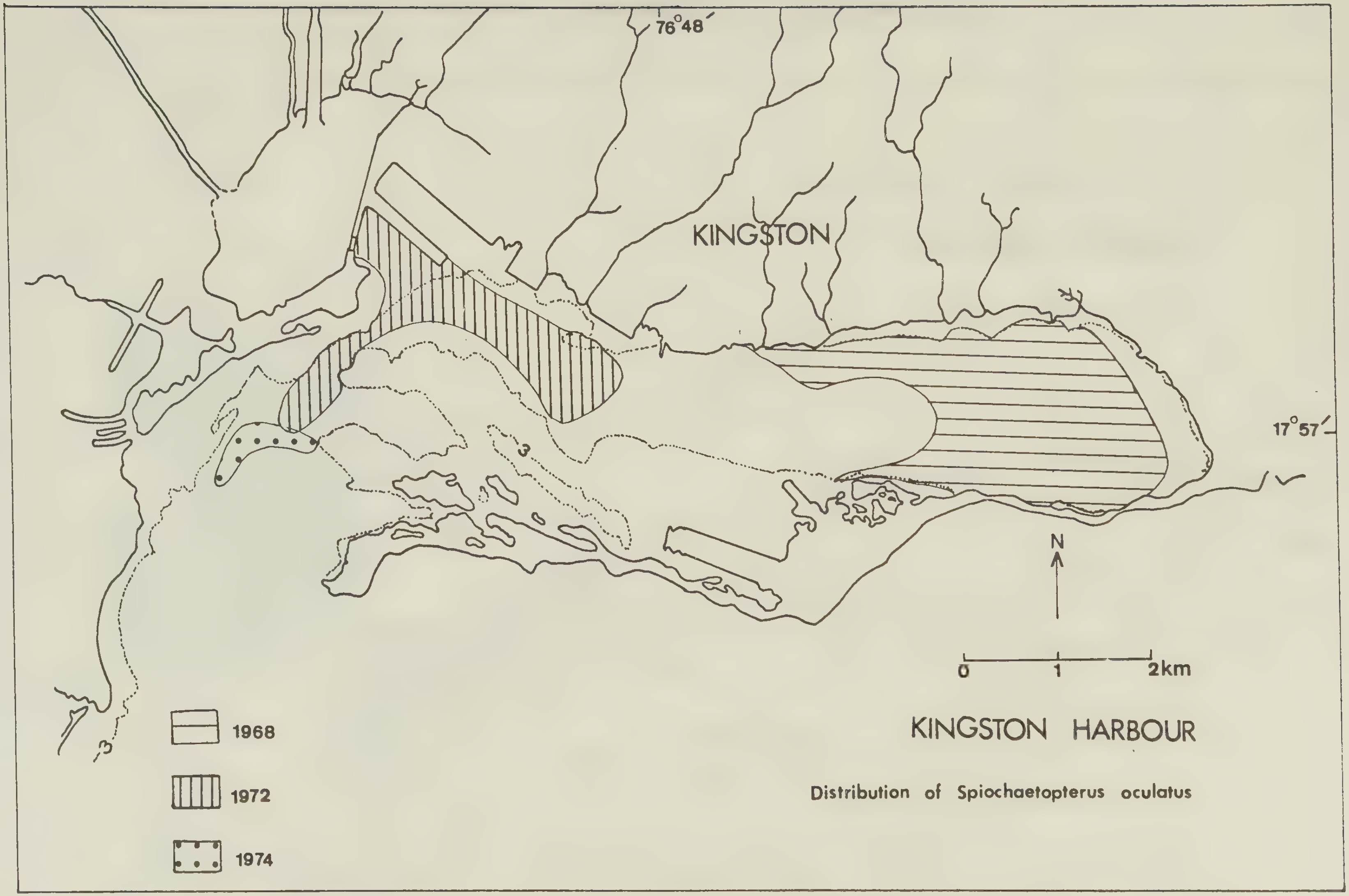
KINGSTON HARBOUR
BENTHIC ZONES
1974
▤ Very polluted zone (0 species per 1/10m²)
▥ Polluted zone (1-5 species per 1/10m²)
∴ Semi - healthy zone (6-10 species per 1/10m²)
░ Healthy zone (> 10 species per 1/10m²)

Fig. 5 Distribution of the benthic zones in Kingston Harbour in 1974, showing the levels of pollution


76°48´
KINGSTON
17°57´
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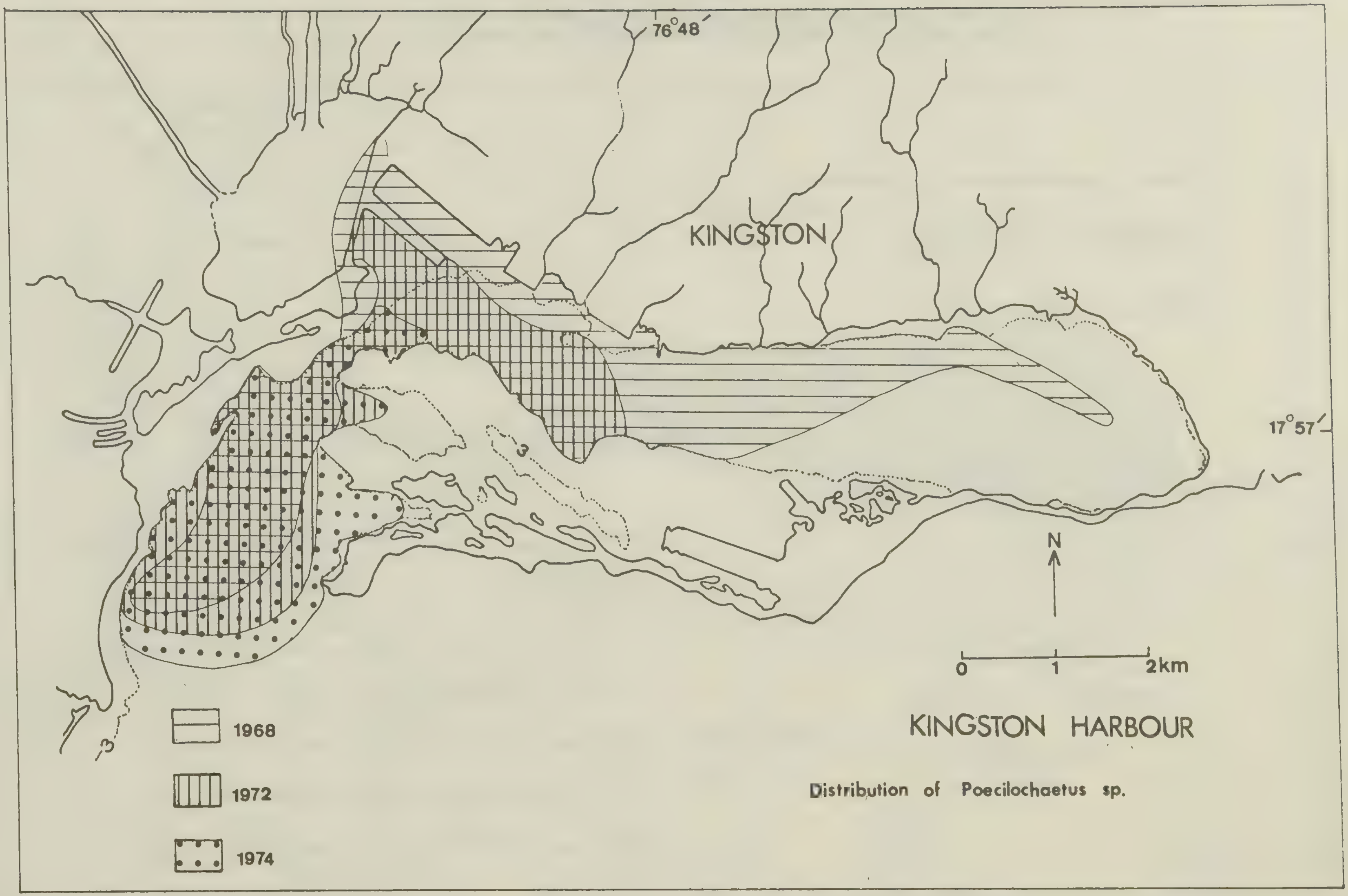
2km
KINGSTON HARBOUR
Distribution of Spiochaetopterus oculatus
1968
1972
1974

Fig. 6 Distribution of *Spiochaetopterus oculatus* in Kingston Harbour in 1968, 1972 and 1974, showing the retreat toward the Outer Harbour and the decrease in area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17°57′
KINGSTON
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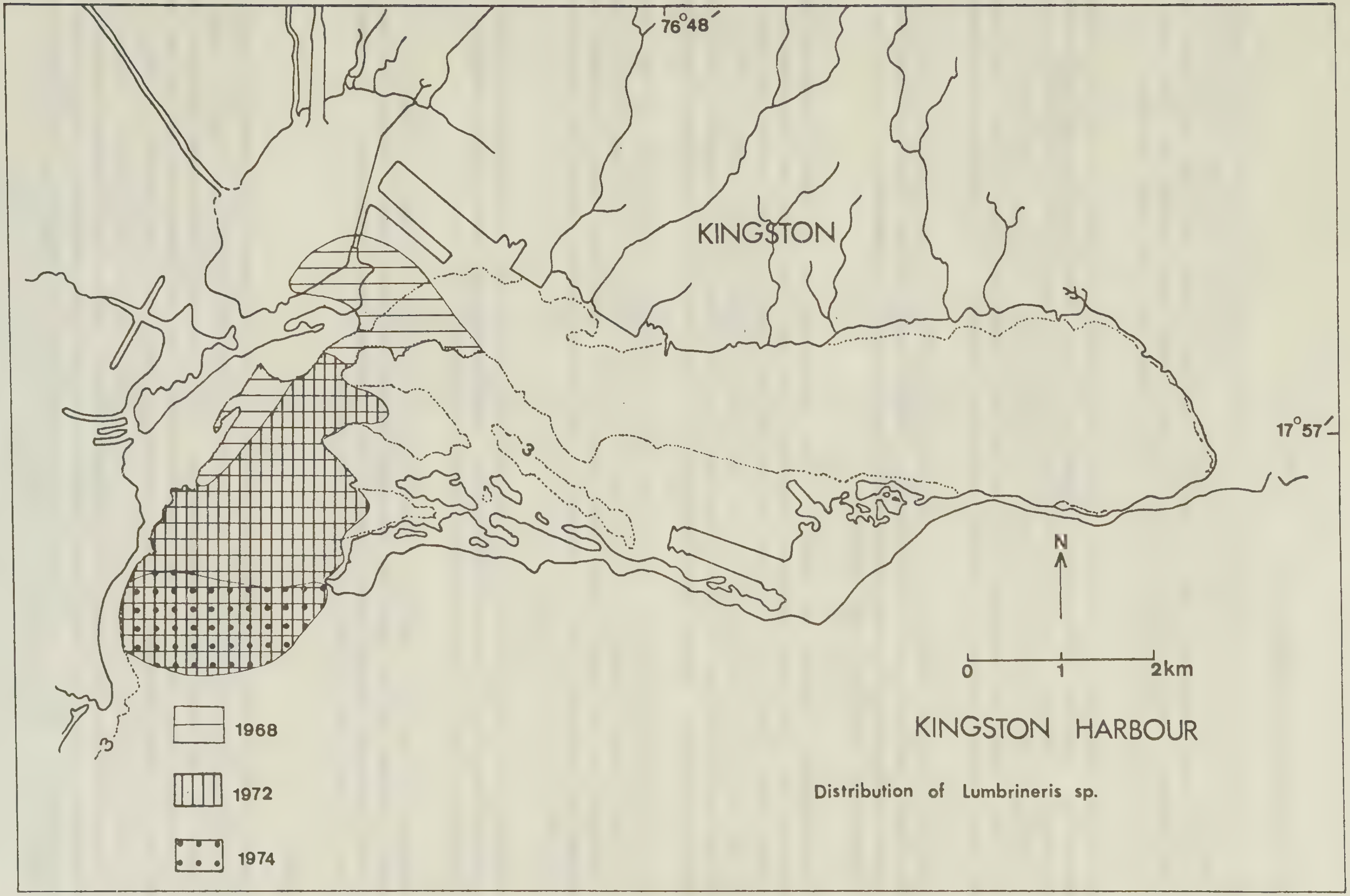
KINGSTON HARBOUR
Distribution of Poecilochaetus sp.
▤ 1968
▥ 1972
⁘ 1974

Fig. 7 Distribution of Poecilochaetus sp. in Kingston Harbour in 1968, 1972 and 1974, showing the decrease in the Inner Harbour and the increase in the Outer Harbour


76°48'
17°57'
KINGSTON
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3
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1
2km
1968
1972
1974
KINGSTON HARBOUR
Distribution of Lumbrineris sp.

Fig. 8 Distribution of *Lumbrineris* sp. in Kingston Harbour in 1968, 1972 and 1974, showing the decrease in the Outer Harbour and the retreat toward the open sea

3.5 Effect of Pollution on Communities

The shift in distribution and density of different species from 1968 to 1974 resulted in obvious changes in the nature of the communities. In the Inner Harbour the two original communities of 1968 were destroyed rapidly and by 1974 the areas they had originally occupied had become abiotic. From a total of 63 species in the Inner Harbour in 1968, only 12 remained by 1974 and these were restricted to a small area near the Outer Harbour.

In Hunts Bay the original 37 species of 1968 were reduced to only 8 in 1974. However, these comprised only 3 species which were originally present and Capitella capitata had become overwhelmingly dominant. In 1972, it comprised 98.5 percent of all individuals and, in 1974, 47.3 percent. Furthermore, the density in Hunts Bay had risen from 219/m^2 in 1968 to 1 555/m^2 in 1974. Thus, the changes in Hunts Bay were profound and, in fact, the original 1968 community had become replaced by another much more typical of a polluted environment.

The changes which have taken place in the Outer Harbour have not been so great, but they have been steady and are now proceeding at a faster rate than in the Inner Harbour and Hunts Bay. These changes may be seen in several features of the community such as its homogeneity, diversity, dominance and density.

In 1968 the community showed no signs of being disturbed and its distribution along a straight line from near the Inner Harbour (station 2) to near the open sea (station 17) followed a normal curve (Fig. 9a). As the effects of pollution spread across the Outer Harbour, stations along the line began to show decreasing similarity so that, by 1974 (Fig. 9d), two groups of station similarities could be discerned and the normal distribution pattern had been destroyed. Hence, the community had lost much of its original homogeneity.

This loss of homogeneity can be correlated with a decrease in diversity of the overall community as the environment deteriorated (Fig. 10) since, as Fig. 11 shows, the decrease in diversity occurred at different rates along the line of stations. Thus, the most rapid decrease occurred at stations 2 and 5, nearest to the Inner Harbour, while the least rapid occurred at station 17, furthest away.

Simultaneously with the decrease in diversity was an increase in dominance (or loss of evenness or equitability). As with diversity, the greatest and most rapid changes occurred at stations 2 and 5, nearest the pollution sources (Fig. 12).

Other changes in the Outer Harbour community have been an increase in density by about 100 percent and a change in the relative proportions of the major taxa. In particular, the polychaetes have increased significantly, while the bivalves have decreased. The other major group, the crustaceans, have been the most stable.

4. DISCUSSION

The changes in the benthos of Kingston Harbour can be related to decreasing oxygen levels resulting from organic pollution. Our studies have indicated how rapidly these changes can occur and to what extent they can go. They have also given some insight into the pattern of changes which soft bottom communities in the Caribbean may undergo as they are subjected to pollution stresses. This knowledge, therefore, has predictive value in that it might help to indicate the course of future events before they occur. Thus, for example, we have predicted that, unless polution abatement occurs in Kingston Harbour, the entire Outer Harbour, along with the Inner Harbour and probably Hunts Bay, might become abiotic at the bottom by 1990. For the decision-makers and implementers, this establishes a definite framework of time in which they must act.

Our studies also provided useful tools for monitoring levels of pollution which could be utilized elsewhere. For example, recognition of indicator species and diversity values for different stress conditions in soft bottom areas should provide simple, but effective

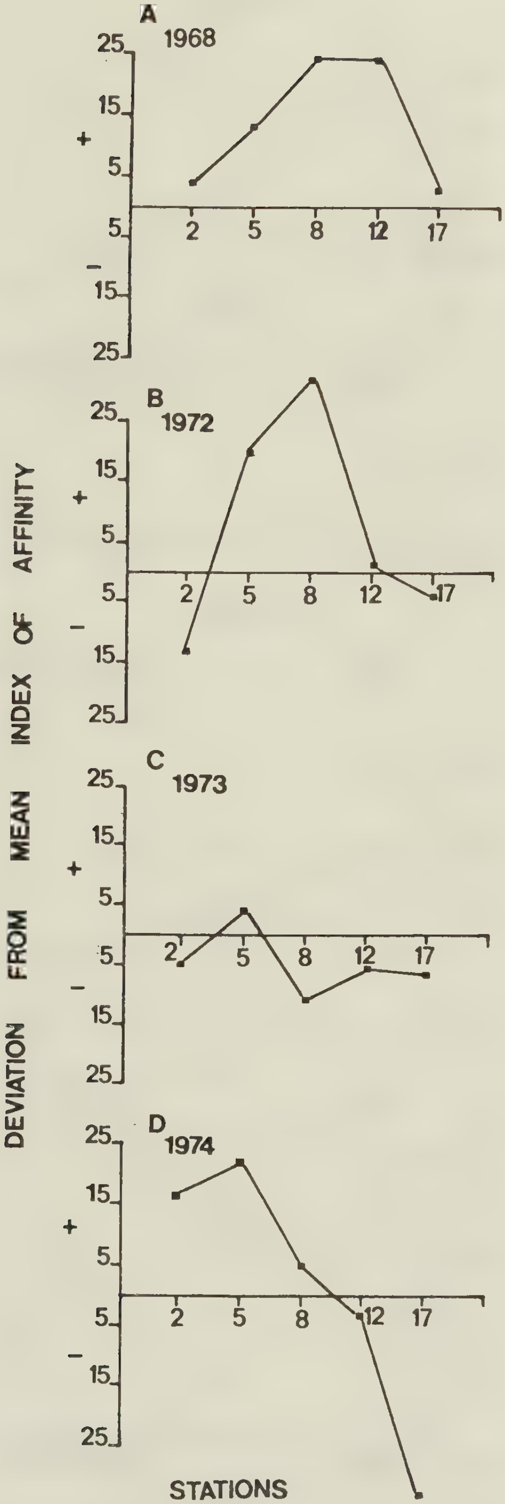

Fig. 9 The distribution of faunal homogeneity in the Outer Harbour for 1968 to 1974, along a line from station 2, nearest the pollution sources, to station 17, furthest away. Faunal homogeneity is expressed as the deviation from the mean index of affinity for each year

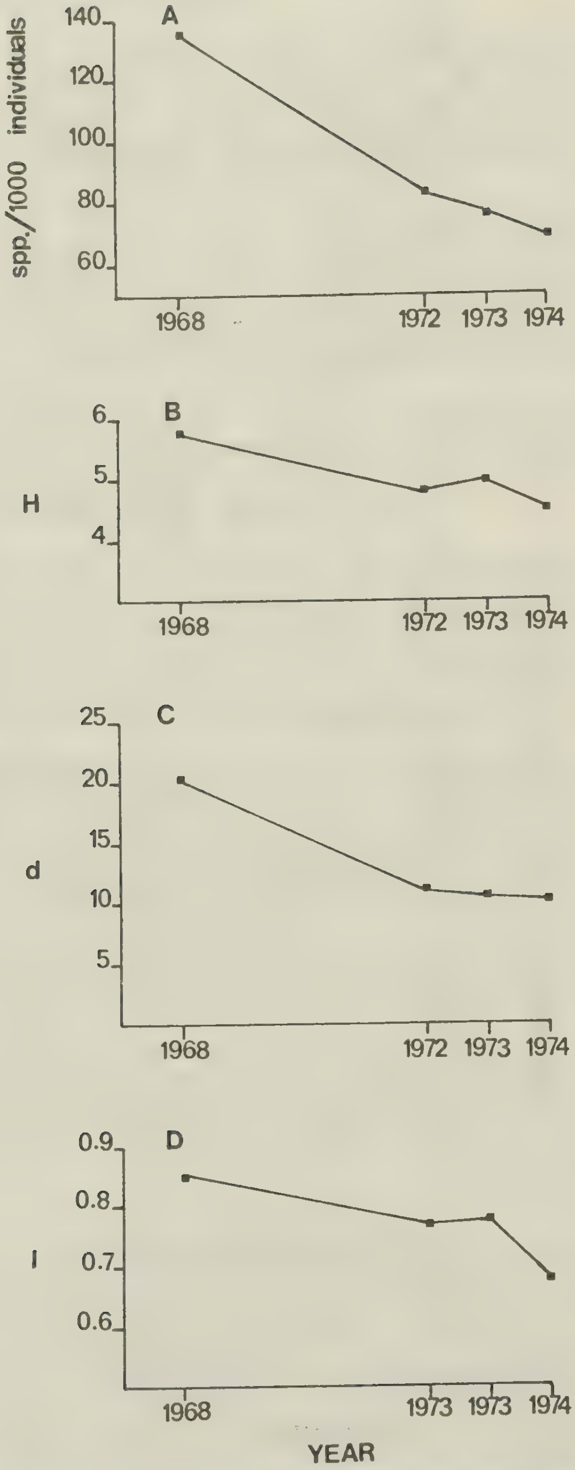

Fig. 10 The decrease in diversity of the Outer Harbour community from 1968 to 1974, expressed by four diversity measures:
(a) Sanders' rarefaction
(b) Shannon-Wiener index (H)
(c) Margalef index (d)
(d) McIntosh index (I)

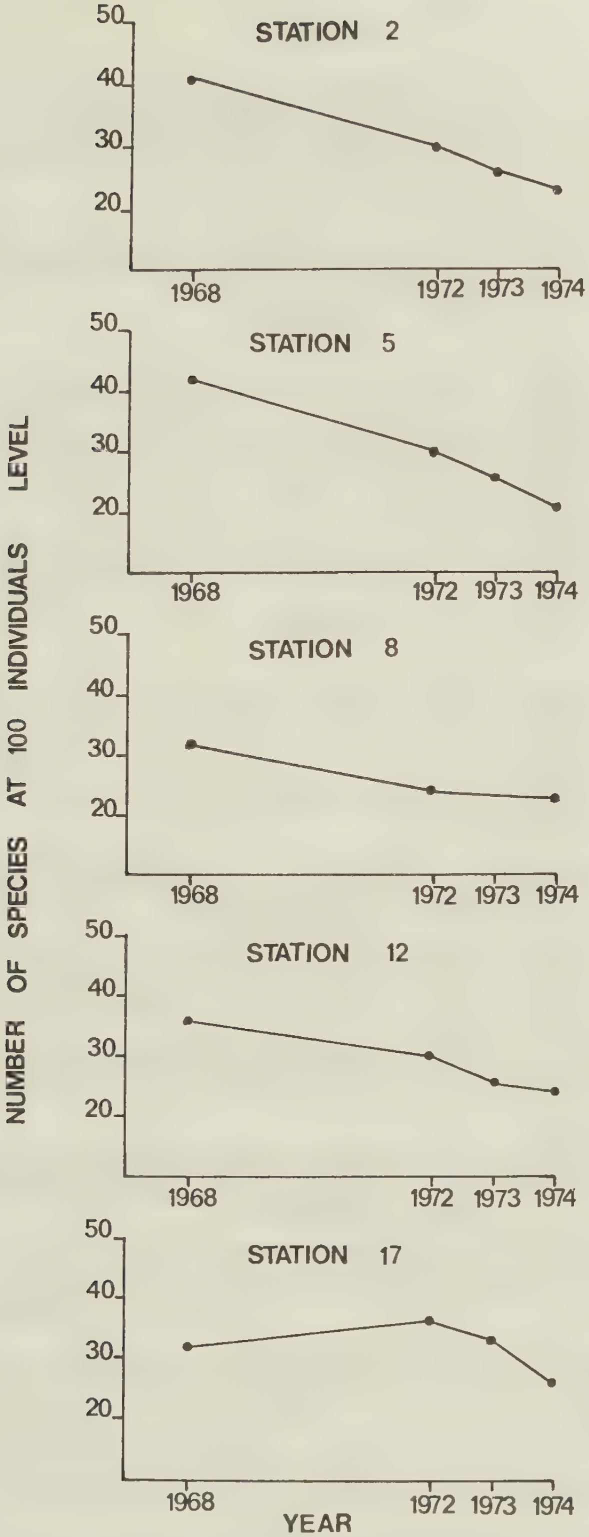

Fig. 11 The decrease in diversity of the Outer Harbour community from 1968 to 1974 along a line from station 2 to station 17, showing the different rates of decrease. Diversity is expressed as the number of species at the 100 individuals level based on Sanders' rarefaction curves

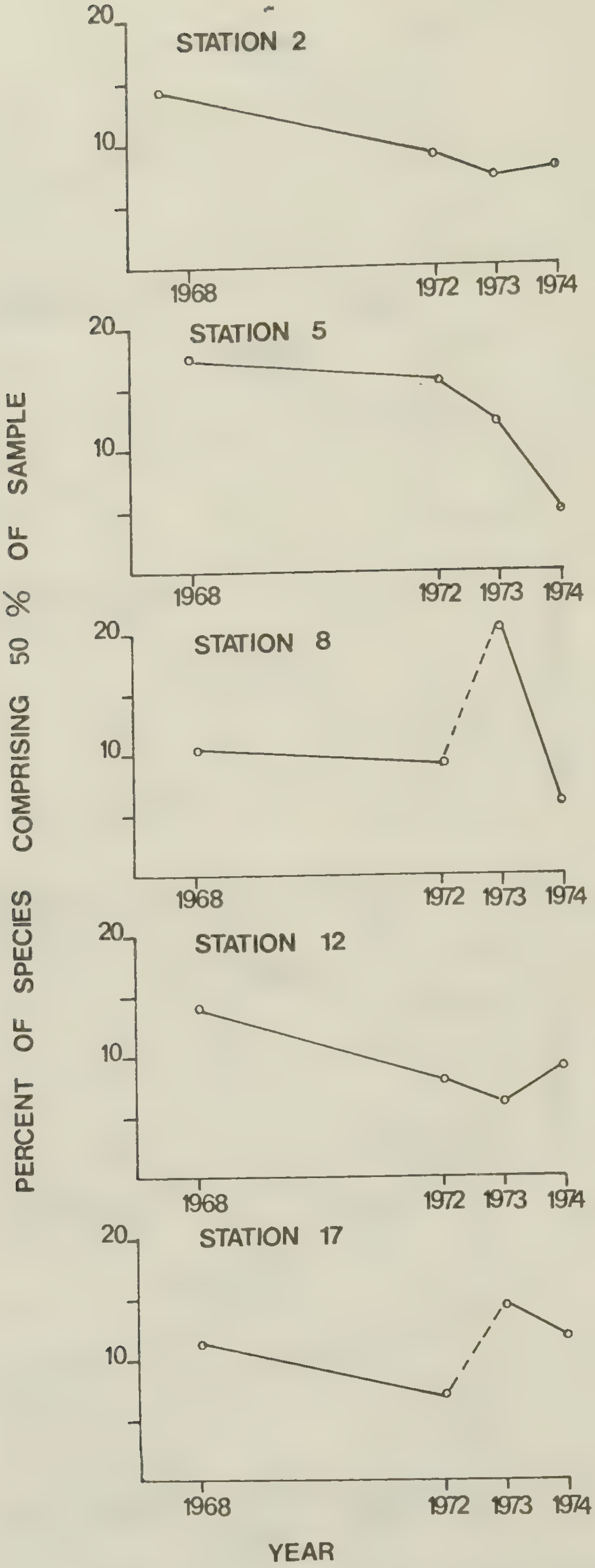

Fig. 12 The increase in dominance (decrease in evenness) of the Outer Harbour community from 1968 to 1974 along a line from station 2 to station 17. Dominance is expressed as the percentage of species comprising 50 percent of the sample

means of assessing pollution in many harbours and bays throughout the Caribbean. Similarly, if such information were available for other kinds of coastal environments (seagrass beds for example), these environments could also be monitored with the minimum of effort and expense.

It is hoped, therefore, that our experience in Kingston Harbour will provide a stimulus for similar studies in a number of different kinds of environment throughout the Caribbean.

5. ACKNOWLEDGEMENTS

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PISCICULTURA EN LAGUNAS COSTERAS: PERSPECTIVAS EN MEXICO

por

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CONTENIDO

1. INTRODUCCION
2. LA FAUNA ICTIOLOGICA LAGUNAR-ESTUARINA
3. SISTEMAS LAGUNARES-ESTUARINOS DE MEXICO
4. PECES MARINOS Y ESTUARINOS CULTIVADOS EN OTRAS LATITUDES
5. PERSPECTIVAS EN MEXICO: MEDIO AMBIENTE Y FAUNA ICTIOLOGICA
6. CONSIDERACIONES FINALES
7. AGRADECIMIENTOS
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Resumen

Se revisan resumidamente los antecedentes actuales de la piscicultura marina y/o estuarina en lagunas costeras de diferentes regiones del mundo, el medio ambiente y la fauna ictiológica utilizada. Esto indica que el cultivo de peces en aguas salobres está bastante extendido en Asia, mucho menos en Europa y muy poco en otras latitudes.

Sobre esta base se discuten las perspectivas de la piscicultura lagunar en México considerando los tipos de lagunas costeras mexicanas, la ecología del medio ambiente y la composición de las comunidades ictiofaunísticas existentes. México posee cuatro unidades oceanográficas principales y según Lankford (1975) las costas presentan 124 lagunas costeras: Océano Pacífico, 48; Golfo de California, 36; Golfo de México, 32; Mar Caribe, 8. Sin embargo, no todas son consideradas "lagunas costeras típicas" con perspectivas de piscicultura lagunar.

La literatura ictiológica lagunar de México es actualmente limitada; no obstante, existen buenos registros de peces lagunares. Las lagunas presentan peces dulceacuícolas, estuarinos propiamente tales, anadromos y catadromos, y diferentes tipos de peces marinos. Esta estructura de las comunidades ictiofaunísticas lagunares varía en su composición y abundancia relativa de especies en relación a las condiciones hidrológicas del sistema, la época del año y la localidad. De acuerdo a la biología y ecología de las especies, existen numerosas de ellas susceptibles de ser cultivadas en México, en especial de las familias Ariidae, Mugilidae, Chanidae, Gerridae, Centropomidae, Cichlidae, Gobiidae y Carangidae.

Abstract

The antecedents of marine and/or estuarine fish culture in coastal lagoons of different regions of the world (environment and the ichthyofauna used) are reviewed. Fish culture in brackish waters is fairly common in Asia, less so in Europe and scarse in other regions of the world.

On the basis of this evidence the perspectives of lagoon fish culture in Mexico are discussed, considering the types of Mexican coastal lagoons, the environmental ecology and the composition of the existing ichthyofaunistic communities. Mexico has four main oceanographic units and according to Lankford (1975) the coast has 124 coastal lagoons: Pacific Ocean, 48; Gulf of California, 36; Gulf of Mexico, 32; and Caribbean Sea, 8. However not all of them are considered "typical coastal lagoons" with possibilities of being used in lagoon fish culture.

The lagoon ichthyological literature of Mexico is limited at the present time; however, good information exists on lagoon fishes. The fish communities of the lagoons comprise fresh-water, estuarine, anadromous and catadromous, and different kinds of marine fishes, with a variation in the composition and relative abundance of species in relationship to the hydrological conditions of the system, the season of the year and the locality. According to the biology and ecology of the fish species a number of them can be cultivated in Mexico, particularly certain species of Ariidae, Mugilidae, Chanidae, Gerridae, Centropomidae, Cichlidae, Gobiidae and Carangidae.

1. INTRODUCCION

Definitivamente la literatura sobre piscicultura lagunar es escasa o excepcional. Los trabajos han sido aislados y corresponden a los primeros intentos en el desarrollo de esta rama. De los más importantes pueden citarse Lunz (1951), Schuster (1952), D'Ancona (1954), De Angelis (1960), FAO/UN (1962), Hora y Pillay (1962), Shelbourne (1964), Tang (1966), Prowse (1966), El-Zarka y Fahmy (1966), Ling (1966), Mol et al., (1968), Finucane (1970), Gunstrom (1970) y Gopalakrishnan (1972).

La mayoría de estos estudios han sido considerados por Bardach et al. (1972) y Pillay, (Ed.) (1972) en dos obras actualmente clásicas en el campo de la acuacultura costera en general.

En México no existen antecedentes sobre piscicultura lagunar; sin embargo, Carranza (1970), Yáñez (en prensa y 1975) y Yáñez et al. (en prensa) han considerado aspectos biológicos preliminares con perspectivas de cultivar peces en lagunas costeras mexicanas.

2. LA FAUNA ICTIOLOGICA LAGUNAR-ESTUARINA

Se acepta que el origen y la distribución de la fauna estuarina derivan parcialmente de la fauna dulceacuícola y parcialmente de la fauna marina; reconociéndose por consiguiente diversos componentes faunísticos, particularmente en el caso de los peces: Gunter (1956), Hedgpeth (1957), McHugh (1967) y Yáñez (en prensa).

La dinámica ecológica del ambiente se refleja en la composición cualitativa y cuantitativa de las comunidades ictiológicas. Estas pueden estar formadas por todos o algunos de los siguientes grupos (Yáñez, en prensa):

(a) peces dulceacuícolas que ocasionalmente penetran en las aguas salobres;
(b) peces anadromos y catadromos, en tránsito;
(c) peces verdaderamente estuarinos, los cuales permanecen toda su vida en el estuario pudiendo penetrar ocasionalmente al mar o al agua dulce;
(d) peces marinos que utilizan el estuario como áreas de crianza o para desovar, pero pasan la mayor parte de su vida en el mar, regresando al estuario estacionalmente;
(e) peces marinos que efectúan visitas al estuario, generalmente como adultos y para alimentarse;
(f) visitantes marinos ocasionales que irregularmente penetran al estuario por diferentes razones, los cuales no son muy importantes en las comunidades nectónicas estuarinas pero su presencia no puede pasar desapercibida (Fig. 1).

Las comunidades varían en su composición y abundancia relativa de especies de acuerdo a:

(i) las condiciones hidrológicas del sistema, consecuencia de
(ii) la estación del año, y
(iii) la localidad dentro del estuario y sus gradientes de salinidad.

Numerosos estudios se han referido, por mucho tiempo, a los diferentes niveles tróficos de la fauna ictiológica. Sin embargo, en estuarios y lagunas costeras estos estudios son excepcionales. Yáñez (1975a) discutiendo los trabajos siguientes además de sus propios estudios (i.e., Hiat, 1947; Thompson, 1957; Yasuda, 1960; Darnell, 1961; Teal, 1962; J.H. Day, 1967; Qasim, 1970; Odum, 1971; Odum y Heald, 1972; J.W. Day et al., 1973; Hodgkin, 1973; Lenanton, 1973; Heald et al., 1974) ha propuesto tres categorías dentro de la trama ictiotrófica de las lagunas costeras. Esto constituye un aspecto ecológico importante en el estudio de la estructura de las comunidades ictiofaunísticas, particularmente cuando se pretende derivar estudios hacia el campo de la piscicultura.

Las tres categorías ictiotróficas corresponden a:

1. Consumidores primarios, categoría en la que se incluyen peces (a) plactófagos - zoo y/o fito - (b) detritívoros, y (c) omnívoros.

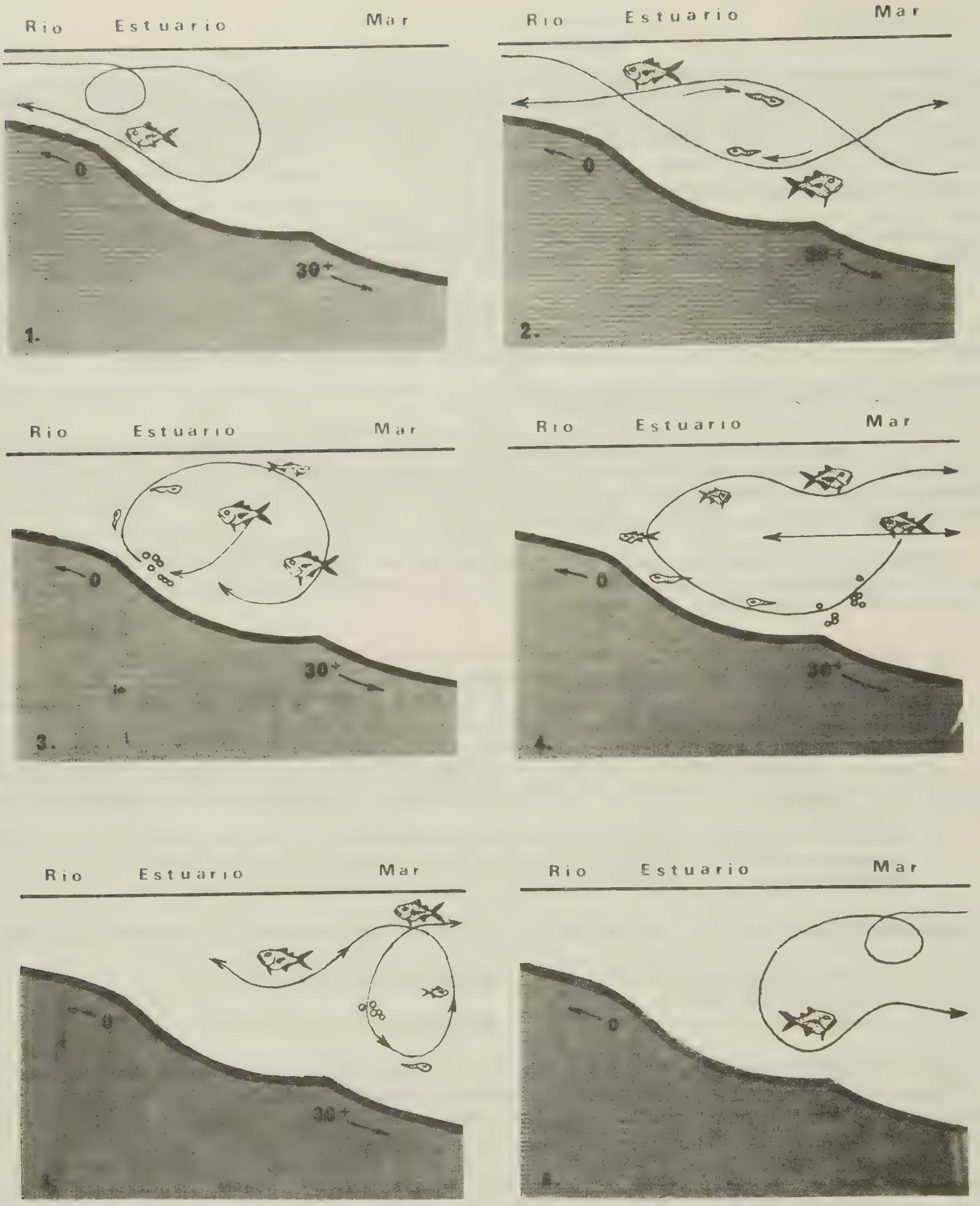

Rio
Estuario
Mar
0
30+
1.
Rio
Estuario
Mar
0
30+
2.
Rio
Estuario
Mar
0
30+
3.
Rio
Estuario
Mar
0
30+
4.
Rio
Estuario
Mar
0
30+
5.
Rio
Estuario
Mar
0
6.

Fig. 1 Composición de las comunidades ictiofaunísticas en estuarios y lagunas costeras (explicación en el texto)

2. Consumidores de segundo orden, categoría en la que se incluyen los peces predominantemente carnívoros, aún cuando pueden incorporar en su dieta algunos vegetales y detritus, pero sin mucha significación cuantitativa;

3. Consumidores de tercer orden, categoría en la que se incluyen peces exclusivamente carnívoros, donde los vegetales y el detritus es un alimento accidental.

Al igual que la variación cualitativa y cuantitativa de los seis componentes nectónicos de las comunidades, en el espacio y en el tiempo; los diferentes niveles tróficos varían asimismo en términos similares. La complejidad de la estructura de las comunidades se encuentra en relación directa con la complejidad de la trama trófica o "food web" (Yáñez y Nugent, 1976).

En piscicultura esto es fundamental puesto que los requerimientos alimenticios de las especies determinan características (a) autoecológicas, (b) biocenóticas y (c) fisiológicas, propias para cada especie. Autoecológicas en el sentido de las adaptaciones morfológicas del aparato digestivo, además de la forma del individuo, sus métodos de capturar el alimento, y sus horas de alimentación. Biocenóticas en el sentido de su rol ecológico dentro de la comunidad y su posición dentro de la trama trófica del ecosistema. Fisiológicas en relación a su capacidad enzimática de digestión, la tasa de absorción, periodicidad de alimentación, y la relación entre la absorción y una nueva ingestión de alimento.

3. SISTEMAS LAGUNARES-ESTUARINOS DE MEXICO

Estos ambientes son ecosistemas críticos para algunos organismos pero al mismo tiempo ideales para otros. En términos generales, son cuerpos de aguas someras de volumenes variables dependiendo de los períodos de seca y de lluvia, con temperaturas elevadas, salinidades muy variables, fondos predominantemente fangosos y características de topografía y superficies muy irregulares.

Sin embargo, existen características que no son compartidas por la mayoría. Las más significativas son:

(a) algunas de ellas presentan un ciclo regular anual de entrada periódica de agua de mar por la abertura de sus barras de acuerdo a un aumento de volumen de agua interna y la consiguiente formación de una cabeza hidrostática que junto con la erosión marina provocan la apertura de la barra, y el posterior cierre de la misma por efectos hidrodinámicos de geología costera y circulación litoral;

(b) otras presentan una barra permanentemente abierta y por consiguiente una influencia marina constante dependiendo su intensidad por las condiciones oceanográficas y/o meteorológicas, y

(c) otras por el contrario permanecen cerradas por muchos años perdiéndose la influencia marina.

La dinámica de estos fenómenos ecológicos naturales determina rangos desde el agua dulce hasta ambientes hipersalinos, dependiendo además de las tasas de precipitación, evaporación, escurrimiento y filtración a través de las barras arenosas. Desde luego esto determina que los estuarios y lagunas costeras correspondan a un ambiente ecológico de cambio donde parece poco apropiado hacer predicciones o pronósticos biológicos a largo plazo.

Numerosos trabajos se han referido a la zona costera de México y a la geología marina de sus lagunas litorales y estuarios. Lankford (1975) ha hecho una síntesis de tales estudios y desde el punto de vista geomorfológico ha propuesto una clasificación separando 124 lagunas costeras de México en cinco tipos diferentes. Sin discutir la clasificación de Lankford (1975) es interesante extractar las regiones costeras mexicanas que el considera (Fig. 2).

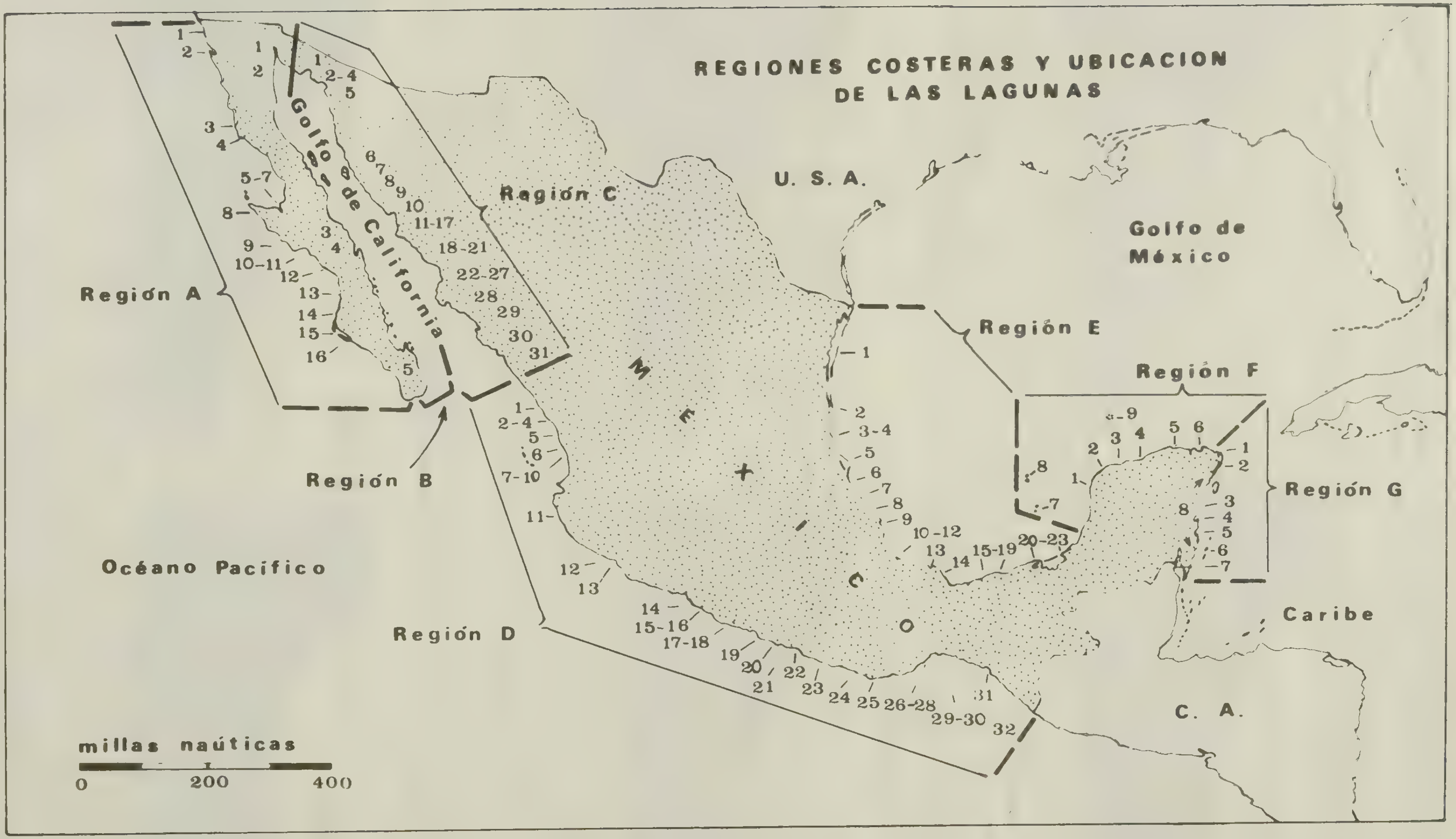

REGIONES COSTERAS Y UBICACION
DE LAS LAGUNAS
U. S. A.
Golfo de
México
Golfo de California
M E X I C O
Región A
Región B
Región C
Región D
Región E
Región F
Región G
Océano Pacífico
Caribe
C. A.
millas naúticas
0
200
400

Fig. 2 Regiones costeras y localización de 123 lagunas costeras mexicanas. Según Lankford (1975)

Región A: Costa del Pacífico; Península de Baja California hasta Cabo San Lucas (16 lagunas costeras)

Región B: Costa del Golfo de California; Península de Baja California hasta Cabo San Lucas (5 lagunas costeras)

Región C: Costa del Golfo de California; Río Colorado hasta Mazatlán (31 lagunas costeras)

Región D: Costa del Pacífico; Mazatlán hasta América Central (32 lagunas costeras)

Región E: Costa del Golfo de México; Estados Unidos hasta Yucatán (23 lagunas costeras)

Región F: Costa del Golfo de México; Yucatán hasta Cabo Catoche (9 lagunas costeras)

Región G: Costa del Caribe; Yucatán, Cabo Catoche hasta América Central (8 lagunas costeras)

Estas 124 depresiones marinas marginales han sido todas referidas como "lagunas costeras" por Lankford (1975) incluyendo designaciones como: bahía, sonda, boca, estero, estuario, caleta, lago, laguna, lagunilla y laguna costera.

Lo más significativo de esto es destacar que México posee 10 000 km de zona costera que comprenden cuatro regiones oceanográficas principales: el Océano Pacífico, el Golfo de California, el Golfo de México y el Mar Caribe. Cifras usadas con mucha frecuencia señalan que la zona costera de México posee 12 555 km^2 de superficie de lagunas costeras o bien 1 567 300 ha de superficie estuárica total (Fig. 3). Estas áreas son real y/o potencialmente productivas, muchas de ellas en estados precarios de explotación, otras irracionalmente explotadas, pero todas en un estado potencial de contaminación futura por los impactos del hombre en el ambiente natural.

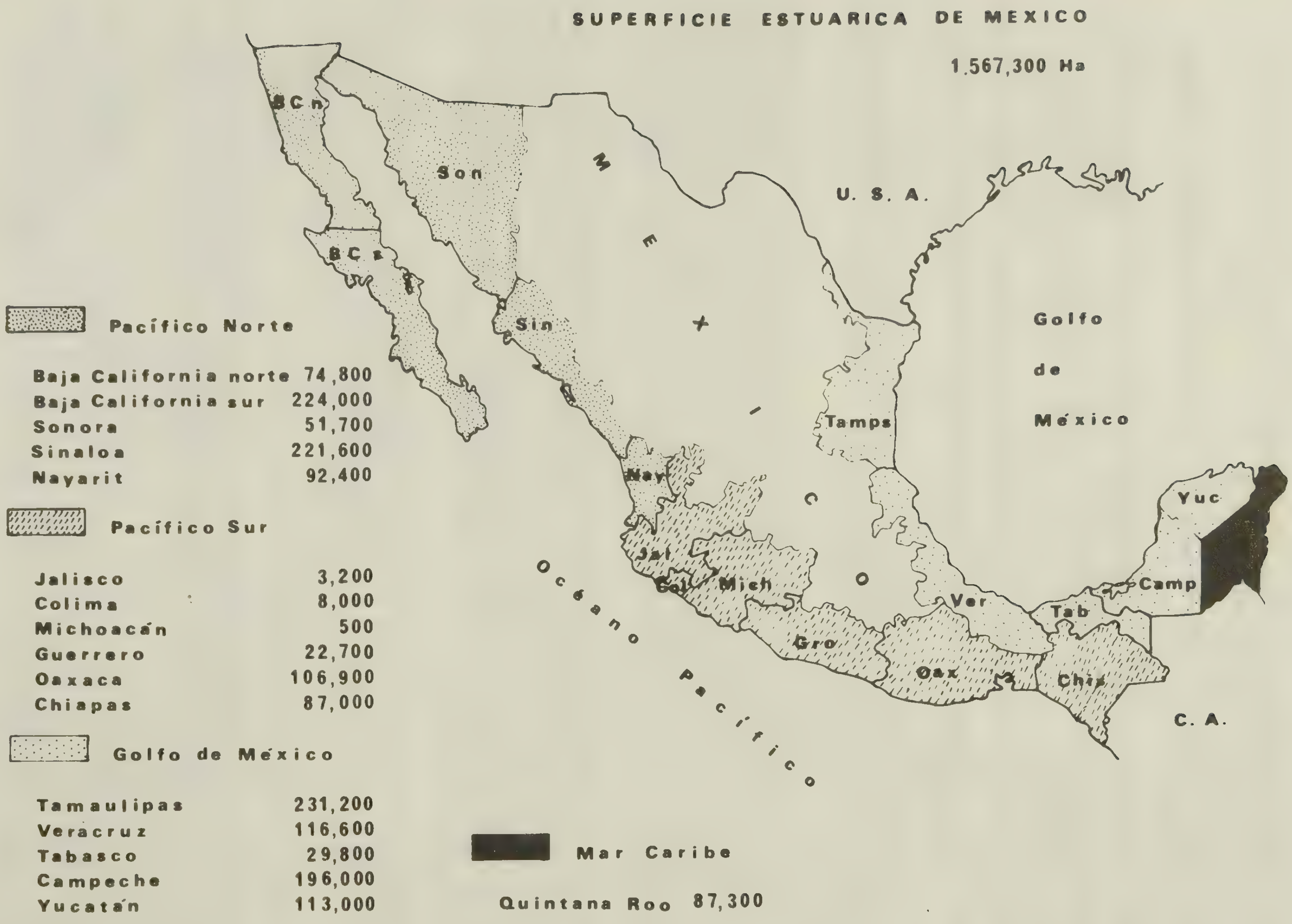
El registro de Lankford (1975) es extenso y muy completo, fundamentalmente por la amplitud de su definición de laguna costera (i.e., "una depresión de la zona costera por debajo del nivel medio de las mareas más altas, teniendo una comunicación con el mar permanente o efímera, pero protegida del mar por algún tipo de barrera".). No obstante, del total de 123 lagunas costeras, las que reunen las características de lagunas costeras típicas con frentes de barreras arenosas son alrededor de 74, clasificadas en el Tipo I (C y D) y en Tipo III (A, B y C) por Lankford (1975).

Probablemente ese tipo de laguna costera son las que presentan mejores perspectivas de piscicultura lagunar. Los cinco tipos de lagunas costeras que Lankford (1975) reconoce para México son: I. Erosión Diferencial, II. Sedimentación Terrígena Diferencial, III Frente de Barrera, IV, Orgánicas y V. Tectónica-Volcánica. Todas referidas a su origen geológico.

4. PECES MARINOS Y ESTUARINOS CULTIVADOS EN OTRAS LATITUDES

Los cultivos de peces marinos y estuarinos que se realizan en la actualidad, a gran escala, pequeña escala, o en forma experimental, son efectuados en países de Europa, Asia, región Indo-Pacífica, EE.UU. y U.R.S.S. Los países latinoamericanos y africanos no han desarrollado en la actualidad piscicultura marina y/o estuarina.

En la Tabla I se resumen las principales localidades donde se desarrolla piscicultura marina y los principales peces que se han utilizado con esos objetivos. Aparentemente la lista es muy extensa; sin embargo, la mayoría de las especies citadas se encuentran en fases experimentales de cultivos y sólo algunas especies son realmente explotadas a gran escala. De estos últimos son más significativos los Mugílidos, Chánidos, Anguíllidos, Carángidos, Látidos, entre otros.


SUPERFICIE ESTUARICA DE MEXICO
1.567,300 Ha
BCn
BCs
Son
Sin
Nay
Jal
Col
Mich
Gro
Oax
Chis
Ver
Tab
Camp
Yuc
Tamps
M E X I C O
U. S. A.
Golfo de México
Océano Pacífico
C. A.

Pacífico Norte	
Baja California norte	74,800
Baja California sur	224,000
Sonora	51,700
Sinaloa	221,600
Nayarit	92,400
Pacífico Sur	
Jalisco	3,200
Colima	8,000
Michoacán	500
Guerrero	22,700
Oaxaca	106,900
Chiapas	87,000
Golfo de México	
Tamaulipas	231,200
Veracruz	116,600
Tabasco	29,800
Campeche	196,000
Yucatán	113,000
Mar Caribe	
Quintana Roo	87,300

Fig. 3 Superficie estuárica de México. Las cuatro regiones principales son consideradas por la Secretaría de Recursos Hidráulicos de México, para el Plan Nacional de Acuacultura

TABLA I

Localidades y principales peces utilizados en piscicultura marina y/o estuarina

TAIWAN:

Mugil cephalus
Mugil dussumieri
Chanos chanos
Anguilla japonica

MALASIA:

Mugil cephalus
Chanos chanos

INDONESIA:

Mugil cephalus
Mugil tade
Mugil dussumieri
Mugil engeli
Chanos chanos
Megalops cyprinoides
Elops hawaiensis
Lates calcarifer
Therapon jarbua
Therapon theraps

VIET-NAM

Chanos chanos
Mugil cephalus
Lates calcarifer

TAILANDIA:

Chanos chanos
Lates calcarifer

PAKISTAN:

Mugil corsula
Mugil cephalus
Mugil tade
Mugil dussumieri
Lates calcarifer
Elops machnata
Alvula vulpes
Monopterus alba
Sphyraena jello
Scatophagus argus
Platosus canius
Platosus anguillaris
Arius leptaspis
Arius maculatus
Etroplus suratensis
Ephinephelus spp.
Therapon jarbua
Therapon theraps
Megalops cyprinoides

COREA:

Plecoglossus altinelis
Anguilla japonica
Crysophrys major

JAPON:

Plecoglossus altinelis
Anguilla japonica
Mugil cephalus
Seriola quinqueradiata
Seriola purpurascens
Lateolabrax japonicus
Ephinephelus spp.
Crysuphrys major
Mylio rubripes

CHINA:

Plecoglossus altinelis
Anguilla japonica
Mugil cephalus
Lateolabrax japonicus

INDIA:

Mugil macrolepis
Mugil traschelli
Mugil corsula
Mugil cephalus
Mugil dussumieri
Mugil tade
Etroplus suratensis
Chanos chanos
Lates calcarifer
Ephinephelus spp.
Therapon jarbua
Therapon theraps
Megalops cyprinoides
Elops machnata
Alvula vulpes
Monopterus alba
Sphyraena jello
Scatophagus argus
Platosus canius
Platosus anguillaris
Arius leptaspis
Arius maculatus

YUGOSLAVIA:

Mugil cephalus
Mugil cheilo
Mugil capito
Mugil saliens

GRECIA:

Mugil cephalus
Mugil cheilo
Mugil capito
Mugil saliens

REP. ARABE DE EGIPTO

Mugil cephalus
Anguilla sp.
Mugil sp.

TUNISIA:

Mugil cephalus

FRANCIA:

Mugil cephalus
Mugil spp.
Chelon labrosus
Lisa ramada
Anguilla anguilla

ISRAEL:

Mugil capito
Mugil auratus
Mugil sp.
Mugil cephalus

REGION MEDITERRANEA GENERAL:

Dicentrarchus labrax
Sparus auratus
Anguilla anguilla
Gobius sp.
Pleuronectes flesus
Solea vulgaris
Bothus podas
Atherina sp.
Atherina mochon
Umbrina cirrhosa
Dentex dentex

NORUEGA:

Gadus morhua
Melanogrammus aeglefinus
Anguilla anguilla

U.R.S.S.

Coregonus albula
Coregonus autumnalis
Coregonus lavaretus

TABLA I (continuación)

U.R.S.S.:

Coregonus meksum
Coregonus nasus
Coregonus peled

REINO UNIDO:

Pleuronectes platessa

SRI LANKA

Etroplus suratensis
Lates calcarifer
Ephinephelus spp.
Therapon jarbua
Therapon theraps
Megalops cyprinoides
Elops machnata
Albula vulpes
Monopterus alba
Sphyraena jello
Scatophagus argus
Platosus canius
Platosus anguillaris
Arius leptaspis
Arius maculatus

BURMA:

Mugil corsula

FILIPINAS:

Chanos chanos
Mugil spp.

BENGALA:

Mugil cephalus
Mugil macrolepis
Mugil dussumieri
Mugil troschelli
Mugil tade
Mugil corsula
Etroplus suratensis
Chanos chanos
Lates calcarifer

KERALA:

Mugil cephalus
Mugil macrolepis
Mugil dussumieri
Mugil troschelli
Mugil tade
Mugil corsula
Etroplus suratensis
Chanos chanos
Lates calcarifer

MADRAS:

Mugil cephalus
Mugil macrolepis
Mugil dussumieri
Mugil troschelli
Mugil tade
Mugil corsula
Etroplus suratensis
Chanos chanos
Lates calcarifer

CHIPRE:

Mugil cephalus
Mugil cheilo
Mugil capito
Mugil saliens

ITALIA:

Mugil cephalus
Mugil capito
Mugil cheilo
Mugil saliens
Anguilla anguilla
Anguilla vulgaris
Dicentrarchus labrax
Solea vulgaris

MEXICO:

Trachinotus carolinus
Trachinotus falcatus

HAWAII (EE.UU.):

Elops hawaiensis
Chanos chanos
Mugil cephalus

EE.UU.:

Mugil cephalus
Mugil spp.
Trachinotus spp.
Cynoscion nebulosus
Leiostomus xanthurus
Sciaenops ocellata
Cynoscion regalis
Micropogon undulatus
Bairdiella chrysura
Orthopristis chrysopterus
Centropistes spp.
Argosargus probatocephalus
Lutjanus griseus
Caranx hippos
Eucinostomus argenteus
Menticirrhus spp.
Lagodon rhomboides
Sphyraena barracuda
Paralichthys spp.

Los países de la región Indo-Pacífica y EE.UU. son los más avanzados en esta rama. Pero algunos países europeos llevan un relativo grado de avance. La información sobre estas actividades en la U.R.S.S. es muy limitada.

5. PERSPECTIVAS EN MEXICO: MEDIO AMBIENTE Y FAUNA ICTIOLOGICA

Las lagunas costeras con mayores perspectivas para intentar desarrollar la piscicultura lagunar, corresponden al Tipo I (C y D) y Tipo III (A, B y C) de la clasificación de Lankford (1975). Estos ecosistemas presentan, la mayoría de ellos, una gran diversidad de habitat para la fauna nectónica, determinado por la presencia de:

(a) fondos arenosos en las bocas;
(b) fondos fangosos hacia el interior;
(c) manglares;
(d) pastos acuáticos;
(e) haloclina o variación drástica de la salinidad en el sentido vertical, etc.

Esto determina la presencia de peces típicos:

(i) pelágicos litorales;
(ii) bentónicos del litoral superior;
(iii) estuarinos, y
(iv) de manglares.

La relación de estos ambientes es muy estrecha en las lagunas costeras y muchas veces es difícil precisar a las comunidades ictiofaunísticas en relación a esos ambientes que normalmente se superponen y/o comparten muchas de las características físicas y químicas del ecosistema.

Yáñez (1975, 1975a y en prensa) ha discutido la conveniencia de realizar estudios sistemáticos sobre las comunidades ictiofaunísticas en lagunas costeras y estuarios (Fig. 4), con la finalidad de desarrollar dos tipos de actividades con una solida y seria base científica:

(a) estudios biológico-pesqueros con perspectivas de cultivos de las especies indígenas de importancia comercial;
(b) estudios biológico-pesqueros con perspectivas de administración racional de las especies de importancia comercial, tanto indígenas como las que visitan cíclicamente el estuario o laguna.

Los ocho puntos de la Fig. 4 no reflejan necesariamente una secuencia obligada pero sí una progresión de complejidad. El paso subsiguiente a los estudios recomendados debe ser la administración del ambiente y sus recursos, para lo cual deben considerarse diversos puntos, entre los más importantes: selección de áreas, construcción de estanques y sistemas de control del nivel del agua, desarrollo de métodos de capturas de peces juveniles, estudios de control de calidad del agua con análisis de la salinidad, el oxígeno y los nutrientes, y análisis del sustrato con estudios de pH, salinidad y nutrientes, estudios de control de la producción primaria, selección de especies adecuadas, conocimiento del cuadro ambiental de las especies en cuestión, control de volumen y calidad del alimento adicional, y control de las enfermedades, etc.

Las perspectivas de la piscicultura lagunar en México son enormes, tanto por su medio ambiente como por las características de su fauna ictiológica. Las consideraciones de la Fig. 4 y los puntos recien arriba mencionados deberían cristalizar en obras de infraestructura como las sugeridas por la Secretaría de Recursos Hidráulicos de México. El paso primordial, consecuencia de esta infraestructura, consiste en poder retener y criar a los peces en lugar de limitarse a capturarlos cuando se dirigen hacia el mar.

1. Reconocimiento del área. Planeación de los muestreos y prospección de la ictiofauna en períodos de seca y lluvia.
2. Evaluación estimativa del potencial íctico. Distribución, diversidad, frecuencia y abundancia.
3. Determinación de los peces dulceacuícolas, estuarinos, anadromos y catadromos, marinos, visitantes esporádicos.
4. Caracterización del ambiente ictiológico lagunar. Pelágico litoral, bentónico litoral superior, estuarino y manglares.
5. Estudio de las relaciones tróficas. Alimentación y habitos alimenticios.
6. Dinámica de las poblaciones. Crecimiento, madurez gonádica y migraciones.
7. El rol ecológico de los peces. Determinación del flujo energético y los niveles tróficos en la ecología del estuario.
8. Estudio biológico pesquero de especies indígenas y visitantes cíclicos de importancia comercial. Perspectiva de cultivos y o explotación racional del recurso.

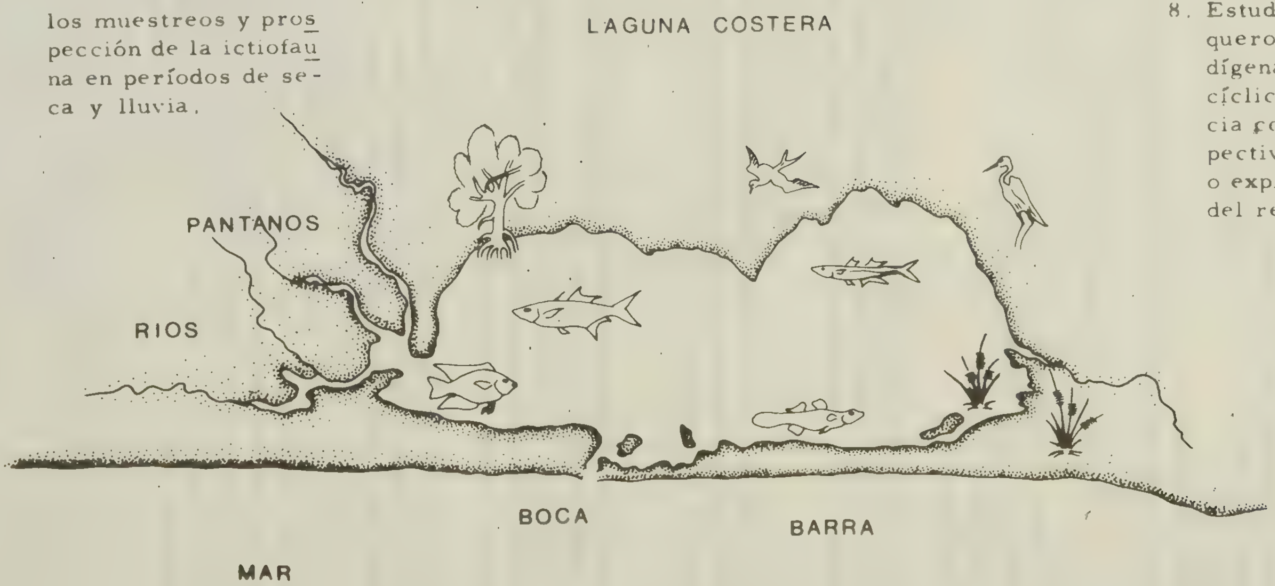


Fig. 4 Progresión de complejidad en el énfasis de las investigaciones ictiológicas lagunares. Según Yáñez (1975a)

Esta forma de cultivos o de producción organizada puede perfeccionarse mediante la fertilización de las aguas y proporcionando alimento adicional a los peces. Además pueden regularse las características físicas y químicas del agua en relación a las necesidades fisiológicas de los peces. Las técnicas utilizadas en cualesquiera explotación de peces exigen varias fases en el proceso, entre las más importantes:

(a) fertilización (sólo ocasionalmente);
(b) siembra;
(c) incubación, y
(d) recolecta o captura (producción).

Los viveros en relación a la piscicultura lagunar se han desarrollado con mucho éxito en Asia (región Indo-Pacífica) con los sistemas llamados "tambaks", en Europa con los sistema llamados "valli", y algunos otros sistemas de "estanques combinados" utilizados en diferentes regiones del mundo. En general, estos permiten la captura masiva de juveniles y el traslado de los peces a diferentes lugares dentro del área del cultivo, conforme crecen.

Revisando la lista de peces marinos y estuarinos que son cultivados en otras latitudes (Tabla I), se puede ver que algunos de ellos se encuentran entre la fauna ictiológica de las lagunas costeras de México. Además la gran mayoría de los géneros existen en las costas de México.

Considerando estos antecedentes y analizando la fauna ictiológica típica de las lagunas costeras mexicanas, se puede resumir que las especies más importantes en México, con perspectivas de piscicultura lagunar son: Ariidae, *Galeichthys caerulescens* (Pacífico); *Arius felis* (Golfo de México y Caribe); Elopidae, *Elops affinis* (Pacífico), *Elops saurus* (Golfo y Caribe); Chanidae, *Chanos chanos* (Pacífico)[1]; Mugilidae, *Mugil curema* (Pacífico, Golfo y Caribe), *Mugil cephalus* (Pacífico, Golfo y Caribe); Gerridae, *Gerres cinereus* (Pacífico, Golfo y Caribe), *Eugerres lineatus* (Pacífico), *Eugerres axillaris* (Pacífico), *Diapterus peruvianus* (Pacífico), *Eugerres plumieri* (Golfo y Caribe), *Diapterus olithostomus* (Golfo y Caribe), *Diapterus rhombeus* (Golfo y Caribe); Centropomidae, *Centropomus robalito* (Pacífico), *Centropomus nigrescens* (Pacífico), *Centropomus poeyi* (Golfo y Caribe), *Centropomus parallelus* (Golfo y Caribe), *Centropomus undecimalis* (Golfo y Caribe); Cichlidae, *Cichlasoma trimaculatu* (Pacífico), *Cichlasoma fenestratum* (Golfo y Caribe?), *Tilapia mossambica*[1]; Gobiidae, *Dormitator latifrons* (Golfo y Caribe); Carangidae, *Trachinotus carolinus* (Golfo y Caribe), *Trachinotus falcatus* (Golfo y Caribe), *Caranx hippos* (Pacífico, Golfo y Caribe).

Considerando que existen numerosas otras especies susceptibles de ser cultivadas en lagunas costeras, probablemente las recién mencionadas tienen mayores perspectivas, por el tamaño, frecuencia, abundancia, biología y ecología relacionada con ecosistemas lagunares-estuarinos (Yáñez, 1976).

6. CONSIDERACIONES FINALES

La productividad y el potencial biológico pesquero de las lagunas costeras y/o estuarios es una situación reconocida desde bastante tiempo. Los principales recursos de estas áreas lo constituyen los peces (Vanucci, 1969); Cárdenas, 1969); sin embargo, sobre ellos existe muy poca investigación orientada a perspectivas de cultivos. Tradicionalmente los estudios sobre recursos lagunares, se han centrado sobre los moluscos especialmente bivalvos (*Crassostrea* spp.) y sobre los camarones peneidos (*Penaeus* spp.), dejándose por mucho tiempo en estado de postergación a los recursos ícticos.

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[1] Especies introducidas, de conocido potencial en otros países, pero sin estudios sistemáticos en México

El estado actual de la piscicultura costera, discutida en parte por Bardach et al. (1972) y Pillay (Ed.) (1972), puede resumirse diciendo que el cultivo de peces en aguas salobres está bastante extendido en Asia (región Indo-Pacífica), mucho menos en Europa y muy poco en las demás regiones del mundo. Huet (1973) considera que las especies Chanos chanos (Chanidae), algunas lisas Mugil spp. (Mugilidae), algunos Anguillidae y probablemente Carangidae, son los peces que han tenido el mejor éxito en prácticas de acualcultura marina y/o estuarina.

No obstante, la fauna ictiológica lagunar-estuarina presenta muchísimas más especies que las discutidas en este trabajo. El elevado trofismo de las lagunas costeras es motivo de atracción para los peces, pero son relativamente pocos los que realizan todo su ciclo biológico en aguas salobres. La pesca en sistemas lagunares depende en mayor medida de especies que realizan migraciones periódicas en las lagunas y que permanecen allí atraídas por la abundancia de alimento. De esa manera la piscicultura lagunar tiene su principal problema en desarrollar técnicas que permitan capturar y retener grandes cantidades de juveniles que penetran cíclicamente al estuario, para alimentarse, protegerse u crecer.

Desde luego, todas las consideraciones expuestas y discutidas a través de este trabajo, deben seguir una estrecha relación con:

(a) perspectivas de administración racional y cultivos de los recursos biológicos y pesqueros;

(b) necesidades de desarrollo socio-económico de la región estudiada.

Todo el complejo proceso ecológico biocenótico (Fig. 4) y la dificultad de su comprensión en términos muy amplios, representan sin duda el principal factor que ha llevado a un estado de postergación en la planificación y la ejecución de los estudios sistemáticos de la fauna ictiológica con perspectivas de cultivos en las lagunas costeras de México, y/o con perspectivas de administración racional de los diferentes recursos biológicos.

La mayor parte de los estudios ictiológicos en las lagunas costeras de México han sido descriptivos (Ramírez, 1952; Darnell, 1962; Alvarez, 1970; Carranza, 1970; Carranza y Amezcua, 1971; Toral, 1971; Amezcua, 1972; González, 1972; Castro, 1974; Castro et al., 1974; Reséndez, 1974 y 1975; Yáñez, 1974; Yáñez y Nugent, 1975), y los menos consideran algunas discusiones biológicas y ecológicas (Yáñez, en prensa, 1975, 1975a, 1976; Yáñez y Nugent, 1976, Yáñez et al., 1975; Amezcua, 1976). Sin embargo, todos corresponden a estudios básicos que deben ser considerados fundamentales por los investigadores que inicien trabajos con perspectivas piscícolas en las lagunas costeras y estuarios mexicanos.

De acuerdo al avance de la piscicultura lagunar o de aguas salobres, en otros países, el principal problema no es ni la reproducción ni la madurez, sino que éste lo constituye la alimentación y el crecimiento. La explicación está en que el principal enfoque en la piscicultura lagunar consiste en poder capturar grandes cantidades de juveniles de peces euritermos y eurihalinos, alimentarlos y hacerlos crecer. Ni las especies de Mugil spp. ni Chanos chanos se reproducen en forma natural en cautiverio.

Tradicionalmente se ha intentado cultivar peces que corresponden a Consumidores Primarios por corresponder a especies más económicas y manejables. Sin embargo, en diferentes países se han utilizado técnicas y métodos de alimentación que han dado buenos resultados con peces Consumidores de Segundo Orden y aún de Tercer orden. Esto es interesante por cuanto la ictiofauna mexicana con perspectivas de cultivos marinos o estuarinos es más abundante entre los Consumidores de Segundo y Tercer orden.

Independiente de su nivel trófico, se puede señalar que los puntos más importantes que debe reunir una especie marina y/o estuarina para intentar cultivarla, deben ser:

(a) conocimiento del cuadro ambiental de la especie

(b) hábitos gregarios;

(c) conocimiento del espectro trófico y hábitos alimenticios naturales de la especie;

(d) alta calidad de su carne;

(e) rangos extremos de tolerancia a la temperatura;

(f) rangos extremos de tolerancia a la salinidad;

(g) resistente a las enfermedades comunes;

(h) aceptabilidad del alimento adicional artificial;

(i) rápido crecimiento.

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